1-1-2012

Object Rivalry: Competition Between incompatible Representations of the Same Object

Nicholas Hindy
University of Pennsylvania, hindy@psych.upenn.edu

Object Rivalry: Competition Between incompatible Representations of the Same Object

Abstract
To understand that an object has changed state during an event, we must represent the `before' and `after' states of that object. Because a physical object cannot be in multiple states at any one moment in time, these `before' and `after' object states are mutually exclusive. In the same way that alternative states of a physical object are mutually exclusive, are cognitive representations of alternative object states also incompatible? If so, comprehension of an object state-change involves interference between the constituent object states. Through a series of functional magnetic resonance imaging experiments, we test the hypothesis that comprehension of object state-change requires the cognitive system to resolve conflict between representationally distinct brain states. We discover that (1) comprehension of an object state-change evokes a neural response in prefrontal cortex that is the same as that found for known forms of conflict, (2) the degree to which an object is described as changing in state predicts the strength of the prefrontal cortex conflict response, (3) the dissimilarity of object states predicts the pattern dissimilarity of visual cortex brain states, and (4) visual cortex pattern dissimilarity predicts the strength of the prefrontal cortex conflict response. Results from these experiments suggest that distinct and incompatible representations of an object compete when representing object state-change. The greater the dissimilarity between described object states, the greater the dissimilarity between rival brain states, and the greater the conflict.

Degree Type
Dissertation

Degree Name
Doctor of Philosophy (PhD)

Graduate Group
Psychology

First Advisor
Sharon L. Thompson-Schill

Keywords
conflict, event representation, fMRI, prefrontal cortex, rivalry, similarity-based interference

Subject Categories
Cognitive Psychology | Neuroscience and Neurobiology | Psychology

OBJECT RIVALRY: COMPETITION BETWEEN INCOMPATIBLE REPRESENTATIONS OF THE SAME OBJECT

Nicholas C. Hindy

A DISSERTATION

in

Psychology

Presented to the Faculties of the University of Pennsylvania

in Partial Fulfillment of the Requirements for the Degree of

Doctor of Philosophy

2012

Supervisor of Dissertation

____

Sharon L. Thompson-Schill, Professor, Psychology

Graduate Group Chairperson

____

John C. Trueswell, Professor, Psychology

Dissertation Committee:
H. Branch Coslett, Professor, Neurology
Michael J. Kahana, Professor, Psychology
Sharon L. Thompson-Schill, Professor, Psychology

ACKNOWLEDGEMENTS

Many wonderful people have contributed to my excitement for studying the mind and brain, and I am thankful to all of the friends and mentors who have made the past five years the most intellectually stimulating and rewarding time of my life.

In particular, I would like to thank my graduate advisor, Sharon Thompson-Schill, for sharing with me her enthusiasm for neuroscience and psychology. Through her thoughtful and nuanced understanding of the methods, mechanics, and goals of cognitive neuroscience, Sharon has shaped my approach to science at every level of analysis. I also would like to thank Gerry Altmann for showing me how to think beyond the methods and constructs most familiar to me. And in practicing the Altmann Exercise, I've learned to turn the tables on "revise and resubmit" simply by listing every logical way in which a reviewer's alternative account of the data can possibly make sense (as well as the corollary predictions that such an account would make). Always by the middle of the list, I see once again that Mary Poppins was right-on: "In every job that must be done there is an element of fun. You find the fun and snap! The job's a game."

I'm also grateful to all of my labmates, classmates, and officemates who make everyday a piece of cake, and who make lab meeting my favorite day of the week. And I thank the National Science Foundation for supporting me financially throughout much of my graduate education, and my undergraduate advisor, Michael Spivey, for getting me hooked on cognitive science.

Finally, I thank my parents for the unwavering support, and my amazing fiancée, Harriet, who always works harder than me.

ABSTRACT

OBJECT RIVALRY: COMPETITION BETWEEN INCOMPATIBLE REPRESENTATIONS OF THE SAME OBJECT

Nicholas C. Hindy

Sharon L. Thompson-Schill

To understand that an object has changed state during an event, we must represent the 'before' and 'after' states of that object. Because a physical object cannot be in multiple states at any one moment in time, these 'before' and 'after' object states are mutually exclusive. In the same way that alternative states of a physical object are mutually exclusive, are cognitive representations of alternative object states also incompatible? If so, comprehension of an object state-change involves interference between the constituent object states. Through a series of functional magnetic resonance imaging experiments, we test the hypothesis that comprehension of object state-change requires the cognitive system to resolve conflict between representationally distinct brain states. We discover that (1) comprehension of an object state-change evokes a neural response in prefrontal cortex that is the same as that found for known forms of conflict, (2) the degree to which an object is described as changing in state predicts the strength of the prefrontal cortex conflict response, (3) the dissimilarity of object states predicts the pattern dissimilarity of visual cortex brain states, and (4) visual cortex pattern dissimilarity predicts the strength of the prefrontal cortex conflict response. Results from these experiments suggest that distinct and incompatible representations of an object compete when representing object state-change. The greater the dissimilarity between described

object states, the greater the dissimilarity between rival brain states, and the greater the conflict.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1: GENERAL INTRODUCTION

> When the identical fact recurs, we must think of it in a fresh manner, see it under a somewhat different angle, apprehend it in different relations from those in which it last appeared.
>
> – *The Principles of Psychology* (William James, 1890)

Recall a pumpkin that you purchased for Halloween. Focus on how the pumpkin looked before you bought it. Now think of how the same pumpkin looked once it was carved and on display. Finally, refocus on how this pumpkin looked in its original uncarved state.

In performing this exercise, many people report difficulty in "letting go" of their strong visual memory of the pumpkin as a decoration, as they attempt to refocus their attention on the image of the same pumpkin in its original state. To guide intuition about this apparent interference between alternative representations of the pumpkin, it may be useful to consider a few observations about this object, as it existed in the world. The first observation is that the pumpkin was in distinct states at distinct points in time; at one point in time the pumpkin was in an uncarved state, while at another point in time the pumpkin was in a carved state. The second observation is that the pumpkin was never in distinct states at a single point in time; at no point in time was the pumpkin in both an uncarved state and a carved state.

Observations about mutually exclusive states of a pumpkin are not far from the popular metaphor of Schrödinger's cat (Schrödinger, 1935). Certainly, Schrödinger's thought experiment was not intended to inform our understanding of the behavior of cats, but instead to inform our understanding of the behavior of electrons. In a similar way, the experiments described here are not intended to inform our understanding of the relationship between incompatible object states, but instead to inform our understanding of the relationship between incompatible brain states. As James' quote suggests, the internal representation of a described object such as a pumpkin has an existence that is distinct from that of the physical object in the world. We take as self-evident that an observable object such as a pumpkin cannot be in multiple states at any one moment in time. We ask whether the brain states which correspond to those alternative object states are similarly incompatible, and if so, whether comprehension of an object state-change thus requires the cognitive system to resolve conflict among representationally distinct brain states.

In the empirical chapters that follow, we use functional magnetic resonance imaging (fMRI) to measure the extent to which alternative object representations compete when an object is changed from its original state. However, we recognize that any productive investigation of a neural system must begin with a description of the system's purpose, as well as a mechanistic framework of cognitive processes through which the neural system achieves this purpose (Marr & Poggio, 1979; Marr, 1982). Therefore, in the remainder of this chapter, we will review literature on how the cognitive system maintains information in working memory, detects conflict between incompatible items of information, and resolves conflict among those items. These concepts will both motivate the forthcoming experiments and guide the interpretation of data in Chapters 2 and 3.

Ambiguity in Language and in the World

Ambiguity is not unique to pumpkins, Schrödinger cats, or electrons. It is present anytime a single object, symbol, or idea maps onto to multiple distinct referents. This correspondence problem is particularly salient in language comprehension. Many words do not have a one-to-one mapping between form and meaning. A long history of psycholinguistic research has demonstrated the presence of ambiguity at nearly every level of linguistic processing. At the most basic levels of speech and text comprehension, multiple phonemes are simultaneously activated when the voice onset time of a stimulus does not strongly cohere to a particular phonetic category (Blumstein, Cooper, Zurif, & Caramazza, 1977; Blumstein, Myers, & Rissman, 2005), and the facility and time course of visual word recognition depends on orthographic neighborhood of the particular word (Coltheart, Davelaar, Jonasson, & Besner, 1977; Seidenberg & McClelland, 1989). Anytime we see a homograph or hear a homonym, we temporarily activate its multiple meanings (Duffy, Morris, & Rayner, 1988; Kintsch, 1988). Likewise, in reading polysemous words such as “fan,” both a summer appliance and an arm-waving admirer may come to mind and compete for attention (Bedny, McGill, & Thompson-Schill, 2008; Klein & Murphy, 2001, 2002). In computational models of lexical ambiguity of polysemous words, distinct mental representations of word senses are viewed as stable states within a semantic space that is shaped by the general frequency of the word sense as well as the specific context in which the word is encountered (Gernsbacher & St John, 2001; Rodd, Gaskell, & Marslen-Wilson, 2004). Context plays an important role in presenting and constraining interpretations of not only homonyms and polysemous words, but also those of language and discourse more generally.

The power of context to produce competition and interference between distinct objects in a visual scene during sentence comprehension has been extensively examined using the Visual World Paradigm (Cooper, 1974; Tanenhaus, Spivey-Knowlton, Eberhard, & Sedivy, 1995). In most uses of this paradigm, eye movements are monitored as subjects view scenes while listening to a description of an event in which objects in the scene take part. Depending on the objects displayed in the scene, subjects predictively pursue incorrect interpretations of a sentence before it is finished, leading to interference between syntactic interpretations, and also between displayed objects (Novick, Trueswell, & Thompson-Schill, 2005). Interference between similar but discrete objects is also reflected in computer-mouse trajectories as subjects click and drag objects on a computer screen during sentence comprehension (Farmer, Cargill, Hindy, Dale, & Spivey, 2007).

The possibility that multiple instances of the *same* object in different states compete and potentially interfere with one another during sentence comprehension has recently been investigated with location change. In a series of eye-tracking experiments, Altmann and Kamide (2009) had subjects view a scene depicting various objects as they listened to a story about the objects in the scene. The story described an event in which the critical object first moved from one location to another, and then that same object was referred to again (e.g., "the woman will move the glass onto the table … then, she will pour the wine into the glass"). When an object was described as being moved, subjects were slightly more likely, when the object was named again, to fixate its presumed destination (e.g., the table) than when the described event left the object unmoved. And when the visual scene was removed *before* the language unfolded (such that subjects first viewed the scene, and then heard the sentences while looking at a blank screen), sentential context fully determined where the eyes were directed. Altmann and Kamide argued that this was because removing the visual depiction of the object eliminated the competition between that depiction and the mental event-based representation of the object. Is there a competitive cost to maintaining multiple representations of an object in the different states through which it has passed? If so, the demands to resolve competition between incompatible interpretations of a linguistic stimulus referring to that object will likely require similar conflict resolution mechanisms studied using other cognitive control tasks, and will likely recruit top-down cognitive control processes mediated by prefrontal cortex.

Ambiguity as a Form of Conflict

The demand to resolve competition between incompatible interpretations of a linguistic stimulus requires us to select relevant information from clutter, and should therefore recruit specific top-down cognitive control processes that are mediated by the prefrontal cortex (Miller & Cohen, 2001; Fuster, 2008). Cognitive control is the ability to override impulses, ignore distractions, and intentionally guide thoughts and actions in the pursuit of internal goals (Miller, 2000). A fundamental aspect of cognitive control is the ability to select a weakly activated representation instead of a stronger representation. Within a distribution-based competition framework for semantic comprehension (e.g, Thompson-Schill & Botvinick, 2006), semantic ambiguity can be understood as a form of conflict. Resolution of semantic conflict may require similar cognitive control mechanisms as do other forms of conflict such as the competition between incompatible task sets, motor responses, and color representations which is induced by the Stroop color-word interference task.

The Stroop interference task is a classic paradigm used to experimentally induce conflict (Stroop, 1935; MacLeod, 1991). For each trial of the Stroop task, subjects are presented with a single color word for which the typeface may not necessarily match the definition of the word (e.g., the word "green" in red typeface). Subjects must indicate the typeface color of the word, and ignore the linguistic meaning of the word. Because word reading is generally fast and automatic, most subjects experience interference between alternative representations of the stimulus word. The Stroop task has been extensively studied at cognitive, neural, and computational levels, and has been shown to involve conflict at multiple levels of representation (MacLeod & MacDonald, 2000; MacLeod, 2005). Manipulations to increase or dampen various forms of conflict in the Stroop task demonstrate conflict that is specific to the selection of semantic alternatives (e.g., Carter, Mintun, & Cohen, 1995; van Veen & Carter, 2005), the selection of motor response (e.g., Pardo, Pardo, Janer, & Raichle, 1990; Zysset, Müller, Lohmann, & Von Cramon, 2001), and the selection of task set (Allport, Styles, & Hsieh, 1994). For instance, to dampen conflict at the level of motor response in a button-press Stroop task, investigators may include "response-ineligible" trials, in which the color term mismatches the typeface color, but the color term is not one of the possible response options (e.g., Milham, Banich, & Barad, 2003). To increase conflict at the level of task representation, investigators may require subjects to switch between color naming and word reading (e.g., Bub, Masson, & Lalonde, 2006). Changes in behavioral performance due to each of these task manipulations are captured in computational models of the Stroop task (e.g., Cohen, Dunbar, & McClelland, 1990; Cohen & Huston, 1994). For instance, by beginning each trial with residual activation of the task-demand units from the previous trial, neural network models simulate the carryover effects when switching between word-reading and color-naming (Gilbert & Shallice, 2002).

Shifting attention from one stimulus dimension to another in the Stroop task may be analogous to the need to shift attention from one object instantiation to another comprehension of an object state-change. Using the functional localization method in fMRI, we may infer the presence of shared conflict-specific neural processes across tasks, based on co-localization of signal change during conflict trials of a Stroop task and state-change trials of an event comprehension task (cf. Saxe, Brett, & Kanwisher, 2006; Fedorenko & Kanwisher, 2009; January, Trueswell, & Thompson-Schill, 2009). However, because the Stroop task involves multiple forms of conflict, the Stroop task by itself is not specific enough to confidently localize the neural response to conflict at a particular processing level. Because we are specifically interested in conflict at the level of semantic representation, we leverage our prior knowledge about the functional anatomy in making inferences about cognitive processes (Henson, 2005; Poldrack, 2006). In particular, we constrain analysis to a relatively well studied area of prefrontal cortex, left posterior ventrolateral prefrontal cortex (pVLPFC).

Left pVLPFC Responds Specifically to Semantic Conflict

Thompson-Schill and colleagues were among the first researchers to use fMRI to extend the field of cognitive control to the domain of semantic retrieval. Thompson-Schill, D'Esposito, Aguirre, and Farah (1997) demonstrated that activity in the left pVLPFC during semantic retrieval is modulated by the cognitive control demand of the task. When generating verbs related to presented nouns, classifying object pictures by their attributes, and comparing words along specific semantic dimensions, the semantic conflict and demand for cognitive control was greater for trials with multiple competing responses than for trials in which there was a single dominant response. Each task and contrast had a unique pattern of activation, but increased percent signal change for all three conflict manipulations overlapped specifically in left pVLPFC. In a follow-up study, patients with damage to left pVLPFC made increased errors in generating verbs for "high conflict" nouns with many associated verbs relative to "low conflict" nouns that had just one strongly associated verb (Thompson-Schill et al., 1998). Moreover, the magnitude of this impairment depended on the extent of damage specific to left pVLPFC. Since then, neuroimaging, patient lesion, and transcranial magnetic stimulation (TMS) studies converge to demonstrate that left pVLPFC is activated during and is necessary for resolving competition amongst incompatible semantic representations (Thompson-Schill, Bedny, & Goldberg, 2005; Badre & Wagner, 2007)

In particular, numerous studies demonstrate an important role for left pVLPFC in selecting context-appropriate meanings of ambiguous words (Metzler, 2001; Bedny, McGill, & Thompson-Schill, 2008). For instance, through measuring subjects' computer-mouse movements during TMS, we demonstrated the necessity of left pVLPFC for contextual disambiguation involving alternative weakly associated targets (Hindy, Hamilton, Houghtling, Coslett, & Thompson-Schill, 2009). For each trial, subjects were displayed two target words. Many of these target words were homonymous or polysemous, such that interpretation depended on the semantic context in which the target appeared. Upon presentation of a stimulus cue, subjects indicated which of the targets was most strongly associated with the cue word. When the target was a strong associate, its ambiguity did not matter, but when the target was a weak associate, contextual disambiguation was important. For instance, the target “cards” is associated with the cue “queen,” but only in the context of playing cards, not in the context of greeting cards and postcards. Upon TMS disruption of left pVLPFC following presentation of a stimulus cue, subjects' mouse-movement trajectories revealed greater deviation toward a distractor when the target and cue had an ambiguous semantic relationship, than when the associative relationship was unambiguous. This ambiguity effect was extinguished when subjects were simultaneously shown both target and cue stimuli, which allowed them to correctly interpret the context of the associative relationship. These results suggest that TMS disrupted the process of contextual disambiguation of the target word, and that left pVLPFC is necessary to resolve semantic competition among stimulus interpretations when the interpretive context of a stimulus is ambiguous, and the appropriate meaning is underdetermined.

Left pVLPFC is also necessary for resolving working memory interference in item recognition tasks such as the recent probes task (Monsell, 1978; Sternberg, 1966). In the recent probes task, subjects are presented with a “target set” of items (e.g., digits, letters, faces, shapes, color patches) followed by a brief delay period during which the subject sees a blank screen and must maintain the target items in working memory. Subsequently, a single “probe” item appears, and the subject must indicate whether the probe item was in the corresponding target set. Interference is induced specifically on “recent negative” trials, in which the probe was not in the target set of the current trial, but was in the target set of the previous trial. For recent negative trials, the subject must ignore the memory of the previous trial to accurately indicate that the probe was not part of the current trial's target set. Evidence from patient lesion deficits, neuroimaging, and TMS appears to converge on the role of the prefrontral cortex in controlling working-memory interference of prior items for recent negative trials (Jonides, Smith, Marshuetz, Koeppe, & Reuter-Lorenz, 1998; D'Esposito, Postle, Jonides, & Smith, 1999; Thompson-Schill et al., 2002; Feredoes, Tononi, & Postle, 2006; Feredoes & Postle, 2010).

In addition to generating verbs with many semantic competitors, selecting context-appropriate meanings of ambiguous words, and resolving working memory interference in item recognition, left pVLPFC has been shown to be critical for overriding misinterpretations of syntactically ambiguous sentences in the Visual World Paradigm discussed above (Novick et al., 2005; January, Trueswell, & Thompson-Schill, 2009and for completing sentences that have multiple alternative responses (Robinson, Blair, & Cipolotti, 1998; Robinson, Shallice, & Cipolotti, 2005). The mountain of evidence suggesting that left pVLPFC resolves competition between semantic representations, makes this brain area a useful marker of semantic conflict in the current studies on the comprehension of object state-change.

Current Studies

Chapter 2 describes two experiments that seek to test whether the same brain regions were activated selectively by sentences referring to an object undergoing state change. In the first experiment, the same object was described as being changed either substantially or minimally by one of two actions (e.g., "the squirrel will sniff/crack the acorn"). In the second experiment, the same action was described as either substantially or minimally changing one of two objects (e.g., “the girl will stomp on the penny/egg”). In each of these experiments, we separately vary the degree to which an object is changed in state by the described action, as well as the imageability of that described action, and measure dissociable components of the neural network that supports event comprehension and object representation. Across the experimental manipulations of action and object, we observe a consistent pattern of results across functionally-defined brain regions suggesting that multiple incompatible representations of an object are in conflict with one another when representing object state-change. Most notably, the greater the difference between the initial state and the end state of an object, the stronger the response in areas of left pVLPFC that are most sensitive to conflict on the individual-subject level.

Based on the conflict-specific response in left pVLPFC we infer the presence of multiple object-state representations in each of the experiments described in Chapter 2. Yet we suspect that the neural substrate of multiple competing object representations includes patterns of distributed activation throughout ventral temporal cortex. Neuroimaging studies of semantic retrieval suggest that knowledge about individual concepts is distributed across networks of overlapping semantic representations in visual and temporal cortices. Many of the same cortical regions that are activated when people see pictures are also activated when they read words. Because the experiments described in Chapter 2 did not permit careful examination of visual object representations, we took a different approach for the experiment described in Chapter 3.

Chapter 3 describes an fMRI experiment for which we used the “information-based” approach of multi-voxel similarity analysis (Weber, Thompson-Schill, Osherson, Haxby, & Parsons, 2009; Kriegeskorte, Mur, & Bandettini, 2008) to measure the distributed neural representations of brain states induced by imagining an object before and after a described action. We find that the physical similarity of incompatible object states before and after a described action predicts not only the strength of the conflict response in left pVLPFC, but also the multi-voxel pattern similarity of the corresponding brain states in feature-selective areas of early visual cortex. Moreover, distributed neural similarity in early visual cortex predicts the strength of the prefrontal cortex conflict response *even better* than separately collected similarity ratings of the incompatible object states. Results suggest that alternative states of an object correspond to distinct visual cortex representations, and that conflict measured in left pVLPFC is mediated by the similarity of distributed representations in visual cortex.

CHAPTER 2: THE EFFECT OF OBJECT STATE-CHANGES ON EVENT PROCESSING: DO OBJECTS COMPETE WITH THEMSELVES?

> A microscopic psychology has arisen . . . carried on by experimental methods, asking of course every moment for introspective data, but eliminating their uncertainty by operating on a large scale and taking statistical means.
>
> – *The Principles of Psychology* (William James, 1890)

Abstract

When an object is described as changing state during an event, do the representations of those states compete? The distinct states they represent cannot co-exist at any one moment in time, yet each representation must be retrievable at the cost of suppressing the other possible object states. We used functional magnetic resonance imaging of human subjects to test whether such competition does occur, and whether this competition between object states recruits brain areas sensitive to other forms of conflict. In Experiment 1, the same object was changed either substantially or minimally by one of two actions. In Experiment 2, the same action either substantially or minimally changed one of two objects. On a subject-specific basis, we identified voxels most responsive to conflict in a Stroop color-word interference task. Voxels in left posterior ventrolateral prefrontal cortex most responsive to Stroop conflict were also responsive to our object state-change manipulation, and were not responsive to the imageability of the described action. In contrast, voxels in left middle frontal gyrus responsive to Stroop conflict were

not responsive even to language, and voxels in left middle temporal gyrus that were responsive to language and imageability were not responsive to object state-change. Results suggest that, when representing object state-change, multiple incompatible representations of an object compete, and the greater the difference between the initial state and the end state of an object, the greater the conflict.

Introduction

Event comprehension requires the ability to keep track of multiple representations of an object as it is altered in state or location. Recent work on language-mediated eye-movements suggests that the mental representation of a described object is dissociable from the perceived object in a concurrently presented visual scene, and suggests further that multiple representations of (all or parts of) the *same* object in different states may compete and interfere with one another during event processing (Altmann & Kamide, 2009).

On reading "*The squirrel will crack the acorn*," we must represent that the acorn existed in distinct states: cracked and intact. If an immediately succeeding sentence reads "*And then, it will lick the acorn*," the cracked state must be retrieved; if, instead, that sentence reads "*But first, it will lick the acorn*," the intact state must be retrieved. Now consider replacing "*The squirrel will crack the acorn*" with "*The squirrel will sniff the acorn*." Regardless of the "but first" or "and then," there is no conflict regarding the representation to be retrieved. We hypothesize that reading about the cracked acorn will recruit brain regions usually associated with conflict resolution, whereas reading about the sniffed acorn will not.

Here, we test the proposal that selecting from amongst distinct states of the same object will selectively recruit prefrontal cortex regions sensitive to semantic conflict, and that this increased activation will overlap on a subject-specific basis with conflict-dependent activation in a standard interference task. Event comprehension trials for each experiment varied in the degree to which a described object was changed in state. In Experiment 1, the same object was changed either substantially or minimally by one of two actions (“crack” or “sniff”). In Experiment 2, the same action (“stomp on”) either substantially or minimally changed one of two objects (an egg or a penny). Conflict-dependent fMRI data collected during a Stroop color-word interference task was used to create subject-specific regions of interest (ROIs) in left posterior ventrolateral prefrontal cortex (pVLPFC), a brain area responsive to semantic conflict (Thompson-Schill, Bedny, & Goldberg, 2005; Thompson-Schill et al., 2005). We additionally examined activation in two other ROIs: 1) voxels in left middle frontal gyrus (MFG) that were responsive to Stroop conflict but unresponsive to sentence comprehension; 2) voxels in left middle temporal gyrus (MTG) responsive to sentence comprehension but unresponsive to Stroop conflict.

In each experiment, the rated degree to which an object changed in state during an event, but not the rated imageability of the described action, parametrically predicted the amplitude of the BOLD response in left pVLPFC voxels most responsive to Stroop conflict. In contrast, object state-change did not predict activation in either left MFG or left MTG; in left MTG we instead observed an effect of action imageability. Across complementary manipulations of action (Expt. 1) and object (Expt. 2), the consistent linear effect of object state-change on conflict-responsive areas of left pVLPFC indicates that multiple states of an object do compete during event processing when the object is changed from its original state.

Materials and Methods

Subjects. Sixteen right-handed native English speakers (9 female), aged 18-28 years, participated in Experiment 1, and a separate sample of 16 right-handed native English speakers (8 female), aged 19-33 years, participated in Experiment 2. Two additional subjects from Experiment 2 were excluded from data analysis and replaced due to unusually poor performance on the event comprehension task; one subject correctly identified fewer than half the catch trials; the other subject had a false-alarm rate that was 10 times the average of all Experiment 2 subjects. All fMRI subjects were paid $20 per hour and were recruited from within the University of Pennsylvania community. Subjects gave informed consent as approved by the University of Pennsylvania Institutional Review Board. Additionally, 522 University of Pennsylvania undergraduate students participated for course credit in an online task used for stimulus norming (273 subjects in Experiment 1; 249 subjects in Experiment 2). All subjects spoke English as a first language.

Event stimuli. Event comprehension items for each experiment consisted of two sentences describing a person or an animal acting upon a single object. Across conditions in each experiment, the object acted upon was either minimally or substantially changed in the first-sentence event. In Experiment 1, we varied the first-sentence action to induce the state-change manipulation; the object acted upon was identical for both "substantial state-change" and "minimal state-change" conditions (e.g., "*The squirrel will crack/sniff the acorn*"). In Experiment 2, we held the action constant across conditions, and varied the object to induce the state-change manipulation (e.g., "*The girl will stomp on the* *penny/egg*”). By separately varying the described action and the described object across Experiments 1 and 2, we avoid changes in pVLPFC activation being due to changes in the verb alone (Expt. 1) or the object alone (Expt. 2; that is, we test whether object state-change drives conflict-dependent pVLPFC activation independent of variations in either action or object. Table 2.1 shows example items from each experiment, along with the object state-change and action imageability ratings corresponding to those items.

EXPERIMENT 1	(object fixed, action varied)		
State-Change Condition		**object state-change**	**action imageability**
minimal	The squirrel will sniff the acorn. And then/But first, it will lick the acorn.	1.87	5.00
substantial	The squirrel will crack the acorn. And then/But first, it will lick the acorn.	5.17	5.68
minimal	The chef will weigh the onion. And then/But first, she will smell the onion.	1.51	5.26
substantial	The chef will chop the onion. And then/But first, she will smell the onion.	5.79	6.00
minimal	The musician will play the piano. And then/But first, he will rave about the piano.	2.47	5.89
substantial	The musician will tune the piano. And then/But first, he will rave about the piano.	4.34	5.13
EXPERIMENT 2	(object varied, action fixed)		
minimal	The girl will stomp on the penny. And then, she will look down at the penny.	1.74	5.55
substantial	The girl will stomp on the egg. And then, she will look down at the egg.	6.20	6.28
minimal	The girl will blow on the dice. And then, she will smile about the dice.	1.72	5.87
substantial	The girl will blow on the dandelion. And then, she will smile about the dandelion.	5.29	6.19
minimal	The karate instructor will kick the foam pad. And then, he will hold up the pad.	2.66	6.07
substantial	The karate instructor will kick the wooden board. And then, he will hold up the board.	5.12	5.98

Table 2.1. Example stimuli from Experiments 1 and 2. Object state-change and action imageability for each sentence of each item was rated on a 7-point scale. fMRI subjects read each item in only one condition. The object state-change and action imageability ratings in the rightmost columns are specific to the first sentence of each item shown.

The first-sentence verb for each item in Experiment 1 was matched across conditions on lexical ambiguity, measured as the number of distinct meanings ($t(238) = 0.75$, $p = .45$; Burke, 2009), and on frequency of use (Brysbaert & New, 2009). The object referred to in each item in Experiment 2 was similarly matched across conditions on both lexical ambiguity ($t(198) = 0.30$, $p = .77$), and frequency ($t(198) = -0.89$, $p = .37$). The action described in the second sentence was identical across conditions in both experiments, and always minimally affected the object. In Experiment 1, the temporal phrase at the beginning of each second sentence was either "but first" or "and then." We included this manipulation to test the additional hypothesis that the "crack…but first" cases would engender increased activity compared to the "crack…and then" cases because of the need to switch the focus from the newly changed state to the previous (unchanged) state. However, we observed the same pattern of neural activity for both the "and then" and "but first" conditions in Experiment 1. (Though not reliable after correcting for multiple comparisons, the largest cluster of increased activation for conditions that required temporal resequencing was in left posterior superior temporal sulcus, an area often linked to speech processing as well as to theory of mind; cf. Hein & Knight, 2008.) In Experiment 2, we therefore kept temporal context constant across items by always beginning the second sentence with "and then." For both experiments, subjects were exposed to all stimuli and all conditions in a fully factorial repeated measures design, but never saw more than one version of each stimulus.

Event ratings. Object state-change and action imageability ratings for the first and second sentence of each item in each experiment were collected through online surveys. Each survey subject rated only one alternative sentence of each item. For object state-change ratings, subjects rated "the degree to which the depicted object will be at all different after the action occurs that it had been before the action occurred." Subjects rated each item on a 7-point scale ranging from "just the same" to "completely changed." For action imageability, subjects rated "how much a sentence brings to mind a clear mental image of a particular action." Subjects rated each item on a 7-point scale ranging from "not imageable at all" to "extremely imageable."

Object state-change and action imageability ratings for the first-sentence events included data from 85 subjects for Experiment 1, and 101 subjects for Experiment 2. The first-sentence event in the "minimal state-change" condition received an average object state-change rating of 1.97 ($SD = 0.57$) in Experiment 1, and 2.78 ($SD = 0.79$) in Experiment 2. The first-sentence event in the "substantial state-change" condition received an average object state-change rating of 4.64 ($SD = 0.84$) in Experiment 1, and 4.96 ($SD = 0.74$) in Experiment 2. Object state-change ratings varied broadly within the "minimal state-change" and "substantial state-change" conditions (Figure 2.1; the overall difference in object state-change between conditions was reliable in each experiment (p's $< .001$). The average first-sentence action imageability rating for the "minimal state-change" condition was 4.89 ($SD = 0.64$) in Experiment 1, and 5.57 ($SD = 0.42$) in Experiment 2. For the "substantial state-change" condition, the average first-sentence action imageability rating was 5.46 ($SD = 0.41$) in Experiment 1, and 5.59 ($SD = 0.47$) in Experiment 2. The difference in action imageability between conditions was reliable in Experiment 1 ($p < .001$), but was not reliable for Experiment 2 ($p = .18$). For both experiments, object state-change correlated with neither frequency nor lexical ambiguity (see above; p's > .4).

Object state-change and action imageability ratings for the second-sentence events included data from 95 subjects for Experiment 1, and 98 subjects for Experiment 2. The second-sentence events of all items in both experiments were designed to involve minimal object state-change. To confirm that there were no differences between conditions, we used a separate online survey to collect object state-change and action imageability ratings for these events. In Experiment 1, the second sentence of each item was identical across conditions, and had an average object state-change rating of 1.90 (*SD* = 0.47), and an average action imageability rating of 4.52 (*SD* = 0.69). For the second sentence in Experiment 2, which had a different object in the "minimal" and "substantial" state-change conditions, the average object state-change rating was 1.69 (*SD* = 0.44) for "minimal state-change" items and 1.74 (*SD* = 0.49) for "substantial state-change" items, while the average action imageability rating was 4.23 (*SD* = 0.83) for "minimal state-change" items, and 4.13 (*SD* = 0.84) for "substantial state-change" items. Experiment 2 items did not reliably differ across conditions in either the object state-change or the action imageability of the second-sentence event (p's > .3).

For each experiment, we additionally collected ratings for the likelihood that the second sentence of each item would follow the first sentence of that item (if that first sentence had been read, for example, in a magazine or newspaper). We used separate online surveys to collect data from 93 subjects for Experiment 1 (which included 4 conditions), and 50 subjects for Experiment 2 (which included 2 conditions). The average likelihood rating across "minimal state-change" event sequences was 4.06 (*SD* = 0.78) in

Experiment 1, and 4.12 (*SD* = 0.90) in Experiment 2. The average likelihood rating for “substantial state-change” event sequences was 4.08 (*SD* = 0.78) in Experiment 1, and 4.28 (*SD* = 0.95) in Experiment 2. There was no statistical difference between state-change conditions of either experiment in the rated likelihood of the event sequences (*p*’s > .2).

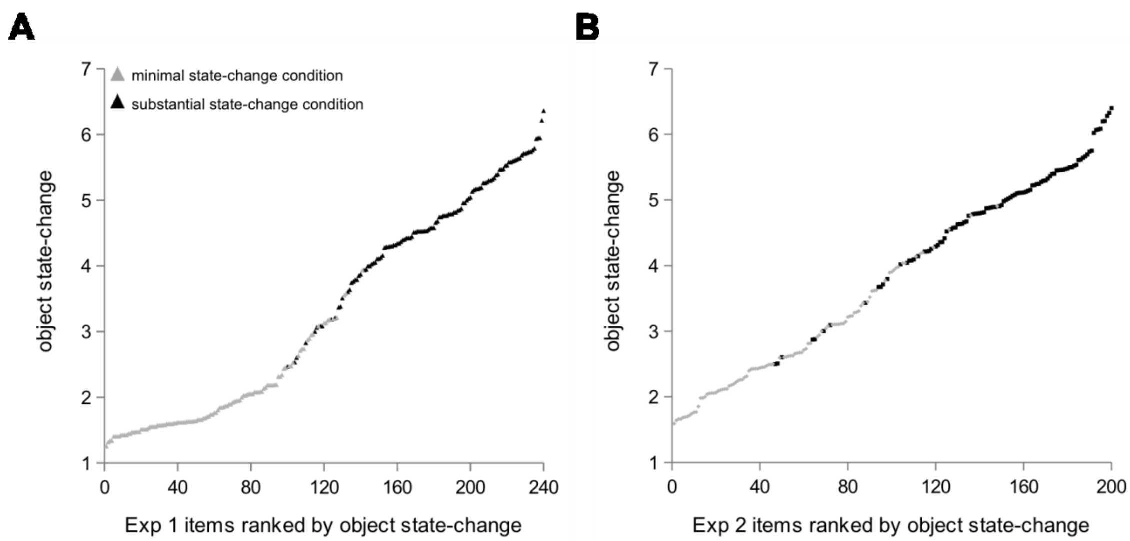

Figure 2.1. Object state-change ratings for the first sentence of each item in the event comprehension task for Experiments 1 and 2. (A) Experiment 1 items, including each item’s “minimal state-change” condition and “substantial state-change” condition, ranked by object state-change. (B) Experiment 2 items ranked by object state-change.

Event comprehension task. The event comprehension task in each fMRI experiment was separated into five runs, with an equal number of trials of each condition in each run. Experiment 1 included 120 experimental trials split across four conditions. Experiment 2 included 100 experimental trials split across two conditions. Additionally, subjects in each experiment read 15 “catch trials” in which the second-sentence event of the trial was implausible given the first-sentence event (e.g., “The mother will eat the sandwich. And then, she will serve the sandwich.”). The trial structure was identical in the two experiments. Each trial lasted six seconds, during which the first sentence was presented for three seconds, followed by the second sentence for three seconds. Subjects pressed the two outer buttons of a keypad when the second-sentence event was implausible given the first-sentence event. Trials were separated by 3 to 15 seconds of jittered fixation, optimized for statistical power using the OptSeq algorithm (http://surfer.nmr.mgh.harvard.edu/optseq/). Stimuli were presented using E-Prime (Psychology Software Tools).

Stroop color-word interference task. After the event comprehension task, subjects in each experiment performed a 10-minute button-press Stroop color identification task, based on previously described procedures (M. P. Milham et al., 2001; January et al., 2009). The response box for this task was restricted to three buttons: yellow, green, and blue. Stimuli included four trial types: response-eligible conflict, response-ineligible conflict, and two groups of neutral trials. Subjects were presented with a single word for each trial, and instructed to press the button corresponding to the typeface color of each word. Conflict trials could be either response-eligible or response-ineligible. For response-eligible conflict trials, the color term matched one of the subject’s possible responses (i.e., yellow, green, or blue), but always mismatched the typeface color. For response-ineligible conflict trials, the color term (orange, brown, or red) mismatched the typeface color, and but was not a possible response. Separate sets of non-color neutral trials (e.g., farmer, stage, tax) were intermixed with either response-eligible conflict trials or response-ineligible conflict trials. Both response-eligible and response-ineligible conflict trial types have previously been demonstrated to induce conflict at non-response levels, while response-eligible conflict trials additionally induce conflict at the level of motor response (M. P. Milham et al., 2001). To optimize power for identifying subject-specific conflict-responsive subregions of left pVLPFC and left MFG, we considered only the main effect of conflict trials versus neutral trials.

Imaging procedure. Structural and functional data were collected on a 3-T Siemens Trio system and an eight-channel array head coil. Structural data included axial T1-weighted localizer images with 160 slices and 1 mm isotropic voxels (TR = 1620 ms, TE = 3.87 ms, TI = 950 ms). Functional data included echo-planar fMRI performed in 44 axial slices and 3 mm isotropic voxels (TR = 3000 ms, TE = 30 ms). Twelve seconds preceded data acquisition in each functional run to approach steady-state magnetization.

Data analysis. Image preprocessing and statistical analyses were performed using AFNI (Cox, 1996). Functional data were sinc interpolated to correct for slice timing, and aligned to the mean of all functional images using a six parameter iterated least squares procedure. The functional data were then registered with each subject's high-resolution anatomical data set, and normalized to a standard template in Talairach space. Finally, functional data were smoothed with an 8 mm FWHM Gaussian kernel, and scaled to percent signal change. Each two-sentence trial was modeled as a six-second boxcar function convolved with a canonical hemodynamic response function, with an additional covariate in the subject-wise parametric analysis to model the degree of object state-change (or action imageability) of the item for each trial. Beta coefficients were estimated using a modified general linear model that included a restricted maximum likelihood estimation of the temporal auto-correlation structure, a polynomial baseline fit, and the motion parameters and global signal as covariates of no interest.

Our analyses are focused on three ROIs, one (pVLPFC) that is our primary region of interest and two (left MFG and left MTG) that serve as controls for our purposes. Stroop-conflict ROIs in both left pVLPFC and left MFG were functionally defined separately for each subject using data obtained during the Stroop color-word interference task. Additionally, each Stroop-conflict ROI was anatomically constrained based on probabilistic anatomical atlases (Eickhoff et al., 2005) transformed into Talairach space. Left pVLPFC was defined as the combination of pars triangularis (Brodmann area 45), pars opercularis (Brodmann area 44), and the anterior half of the inferior frontal sulcus. Across subjects from both experiments, the anatomical definition of left pVLPFC included an average of 784 voxels (SD = 35). Left MFG included portions of Brodmann areas 6, 9, 10, and 46. Across subjects from both experiments, the anatomical definition of left MFG included an average of 962 voxels (SD = 40). Across subjects from both experiments, the anatomical definition of left MTG included an average of 644 voxels (SD = 33). Within these broad anatomical boundaries, each Stroop-conflict ROI comprised the 50 voxels with the highest t-statistics in a within-subject contrast of conflict trials versus neutral trials in the Stroop color-word interference task, while the sentence-comprehension ROI comprised the 50 left MTG voxels with the highest t-statistics in a within-subject contrast of all event comprehension trials (averaged across conditions) versus baseline. Although analyses are reported for ROIs of 50 voxels, the same statistical patterns were consistently observed across a broad range of ROI sizes. All statistical tests for each ROI were evaluated at the two-tailed .05 level of significance. Finally, we assessed the object state-change effect in each voxel across the whole brain, corrected for multiple comparisons, which we report at the end of the Results.

Results

Stroop color-word interference task

Across Experiments 1 and 2, subjects correctly answered 98% of all trials. The average response time was 706 ms for conflict trials and 656 ms for neutral trials ($t(31) = 6.60$, $p < .001$). In a group-level contrast that included all subjects from both experiments, the most reliable cluster of voxels with an activation difference between conflict trials and neutral trials was centered between the inferior frontal gyrus (pars triangularis) and the inferior frontal sulcus of left pVLPFC (Figure 2A). Additional clusters of increased activation for conflict trials relative to neutral trials were observed in left MFG and left intraparietal sulcus.

Stroop-conflict ROI in left pVLPFC

To determine voxels most responsive to conflict on an individual subject level, we identified for each subject the 50 left pVLPFC voxels with the highest *t*-statistics in a contrast of conflict trials versus neutral trials in the Stroop interference task. The location of the top 50 conflict-responsive voxels varied widely across subjects, with slightly more cross-subject overlap in the most posterior area of left pVLPFC, at the junction of pars triangularis, pars opercularis, and the inferior frontal sulcus (Figure 2B). Within each subject-specific Stroop-conflict ROI in left pVLPFC, we examined the effect of object state-change on the amplitude of the BOLD signal.

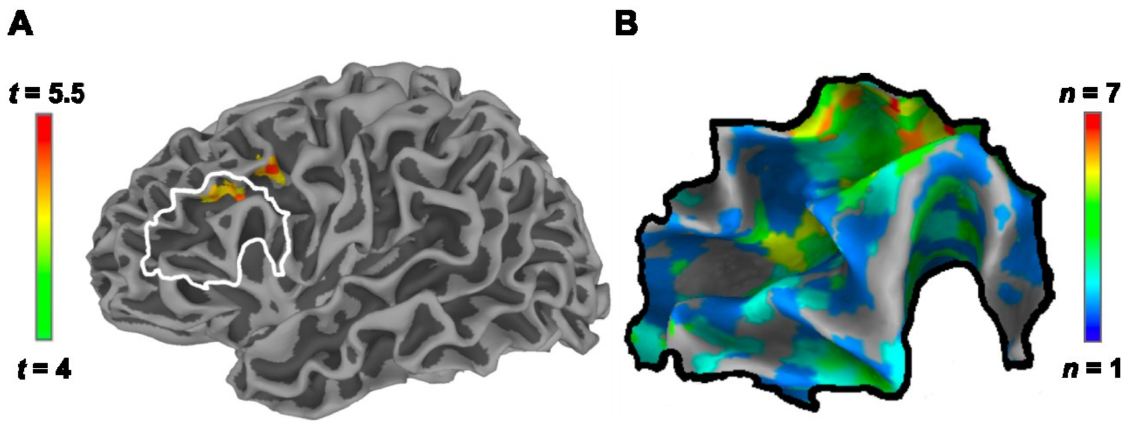

Figure 2.2. Stroop-conflict ROI in left pVLPFC. (A) Whole-brain group-level contrast of conflict trials versus neutral trials in the Stroop color-word interference task, thresholded at a corrected alpha of *p* < .01, and displayed on a partially inflated Talairach surface; left pVLPFC is outlined in white. (B) Probabilistic overlap map of the subject-specific Stroop-conflict ROIs in left pVLPFC. Each subject-specific ROI included the 50 left pVLPFC with the highest within-subject *t*-statistics for the Stroop contrast. The left pVLPFC voxel with the greatest overlap across subjects included 7 of the 32 total subjects from both Experiment 1 and Experiment 2.

Experiment 1 event comprehension (object fixed, action varied)

Subjects correctly identified 97% of catch trials in the Experiment 1 event comprehension task, and committed false alarms (i.e., classifying a non-catch trial as implausible) on fewer than 2% of experimental trials. There was a slightly but reliably greater number of false alarms for the substantial state-change trials (2%) than for the minimal state-change trials (1%; $t(15) = 2.46$, $p = .03$). Due to the small numbers involved, this difference was also tested in a chi-square test, and was also found to be significant (χ-square = 9.62, $p = .002$). False alarm trials, along with catch trials, were coded separately for all fMRI analyses.

The average signal change across all sentence conditions was reliably above baseline in the left pVLPFC Stroop-conflict ROI ($t(15) = 8.59$, $p < .001$), indicating that this ROI was generally responsive during sentence comprehension. Because action imageability ratings were correlated with object state-change ($r = .50$), we removed variance predicted by the action imageability ratings before comparing the “substantial state-change” and “minimal state-change” conditions, though including action imageability as a covariate did not influence the reliability of any effects. A significant main effect of object state-change emerged within the left pVLPFC Stroop-conflict ROI ($t(15) = 2.50$, $p = .02$; Figure 2.3A), but there was no effect of temporal order (“and then” versus “but first”) and no interaction (p’s > .4). Next, we used the data from ratings of object state-change and action imageability to examine the relationship between these stimulus dimensions and signal change within the left pVLPFC Stroop-conflict ROI. Analyses separately tested the reliability of object state-change and action imageability effects across subjects and across items. Because we did not find an effect of the temporal context of the second sentence (either “but first” or “and then”), we averaged across these temporal conditions in each Experiment 1 parametric analysis that used the object state-change or action imageability ratings.

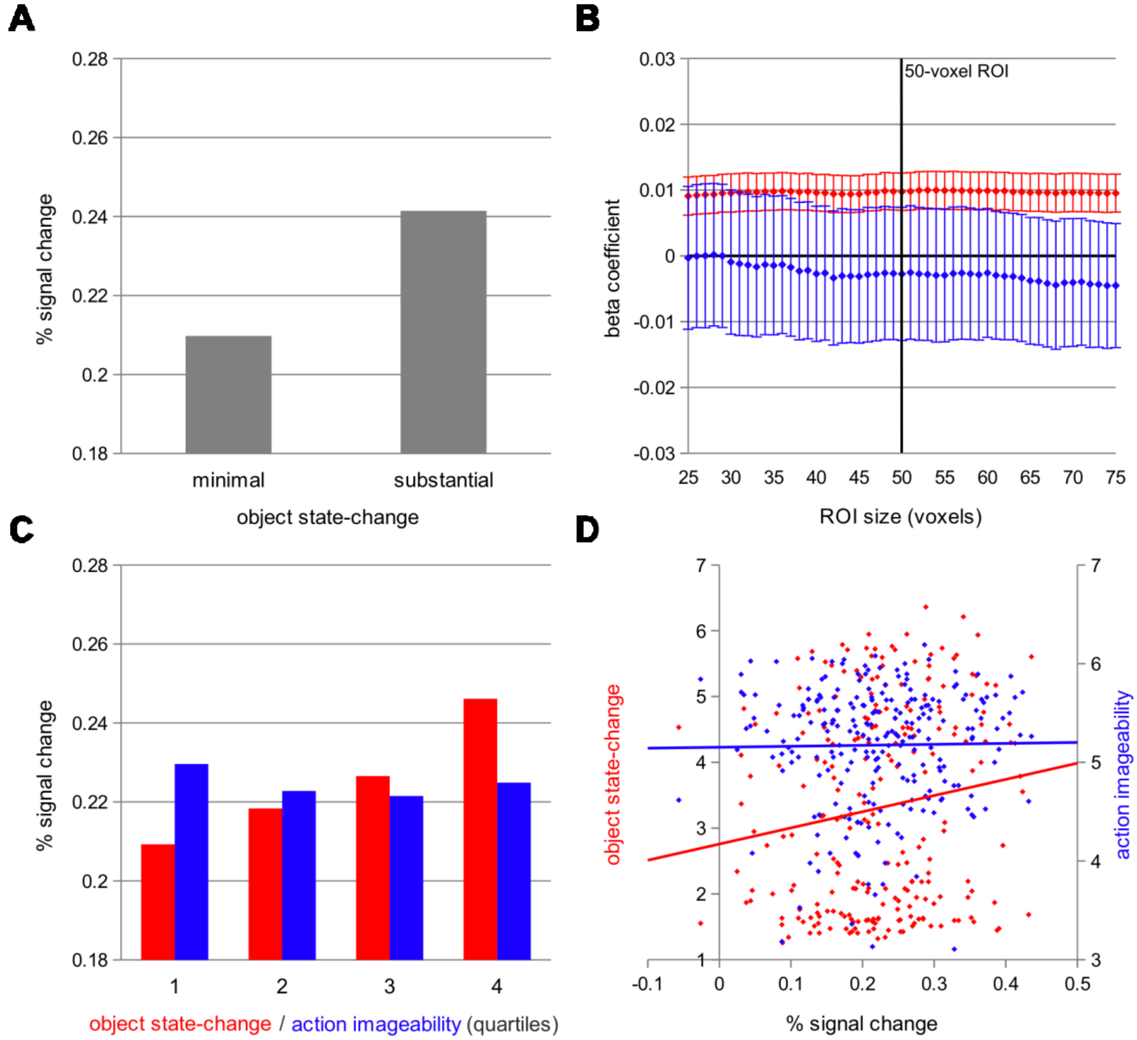

Figure 2.3. Experiment 1 left pVLPFC Stroop-conflict ROI analysis. (A) Percent signal change plots from a categorical analysis of the "minimal state-change" and "substantial state-change" conditions. (B) Beta coefficients across a broad range of ROI sizes from a subject-wise parametric analysis of voxel activation predicted by object state-change and action imageability stimulus ratings. A vertical line indicates the 50-voxel threshold for each subject's left pVLPFC Stroop-conflict ROI. Error bars indicate ± 1 standard error of the mean. (C) Binned quartile visualization of the subject-wise parametric analysis. (D) Item analysis of stimulus ratings and voxel activation. Item-specific activation, averaged across subjects, in the left pVLPFC Stroop-conflict ROI is plotted against the object state-change and action imageability stimulus ratings.

In a subject-wise parametric analysis, we measured the extent to which, for each subject, the BOLD signal amplitude within the left pVLPFC Stroop-conflict ROI varied in proportion to either object state-change or action imageability. Data were separately modeled for each subject, using one covariate to model each trial presentation, and a second covariate to model the degree of object state-change (or action imageability) of the item for each trial. Estimation of these beta coefficients converged with results from the categorical analyses above, as object state-change stimulus ratings reliably predicted left pVLPFC signal amplitude ($t(15) = 3.44$, $p = .004$). In contrast, action imageability ratings did not reliably predict left pVLPFC signal amplitude ($t(15) = -0.27$, $p = .79$). Moreover, across a broad range of ROI sizes, object state-change reliably predicted signal amplitude within the left pVLPFC Stroop-conflict ROI, while action imageability did not reliably predict activation (Figure 2.3B). Interestingly, while object state-change consistently predicted left pVLPFC signal amplitude, both across subjects and across ROI sizes, there was much greater variance across subjects in the degree to which the action imageability ratings predicted signal. This may reflect individual experiential differences across subjects. To further visualize this dissociation, we binned the items into quartiles according to either the object state-change or the action imageability ratings of the stimuli (Figure 2.3C).

In an item-wise analysis, we measured the extent to which, for each item averaged across subjects, BOLD signal amplitude within the left pVLPFC Stroop-conflict ROI could be predicted by the stimulus ratings. Data were separately modeled for each trial, and then individual beta coefficients were binned by item across subjects. Because each of the 120 items included 2 state-change versions (i.e., "substantial state-change" and "minimal state-change"), and because each subject read only one version of each item, there were 238 degrees of freedom in the Experiment 1 item analysis, and the average percent signal change of each item was composed of data from 8 of the 16 subjects. Object state-change ratings correlated with percent signal change in the left pVLPFC Stroop-conflict ROI ($r(238) = .15$, $p = .02$), while action imageability ratings did not predict signal ($r(238) = .01$, $p = .82$; Figure 2.3D).

Experiment 2 event comprehension (object varied, action fixed)

Subjects correctly identified 92% of catch trials in the Experiment 2 event comprehension task, and committed false alarms on 2% of experimental trials, with an equal number of false alarms for the substantial state-change and minimal state-change conditions ($t(15) = 1.21$, $p = .25$; χ-square = 1.87, $p = .17$). As in Experiment 1, false alarm trials were coded separately, along with catch trials, for all fMRI analyses.

All Experiment 1 effects of object state-change on activation in the left pVLPFC Stroop-conflict ROI replicated in Experiment 2. As in Experiment 1, the average percent signal change across conditions was reliably different from baseline ($t(15) = 6.65$, $p < .001$). With action imageability covaried out, there was a reliable categorical effect of the “substantial state-change” condition versus the “minimal state-change” condition ($t(15) = 3.03$, $p = .008$; Figure 2.4A). In the subject-wise parametric analysis, object state-change reliably predicted ROI activation ($t(15) = 2.98$, $p = .009$), while action imageability did not ($t(15) = -0.37$, $p = .71$). As in Experiment 1, this pattern was reliable across a broad range of ROI sizes, with greater variance across subjects in the action imageability parameter estimate than in the object state-change parameter estimate

(Figure 2.4B). In the item-wise analysis, object state-change ratings reliably predicted percent signal change in the left pVLPFC Stroop-conflict ROI ($r(198) = .24$, $p < .001$), while action imageablity did not predict signal change ($r(198) = .00$, $p = .98$; Figure 2.4D).

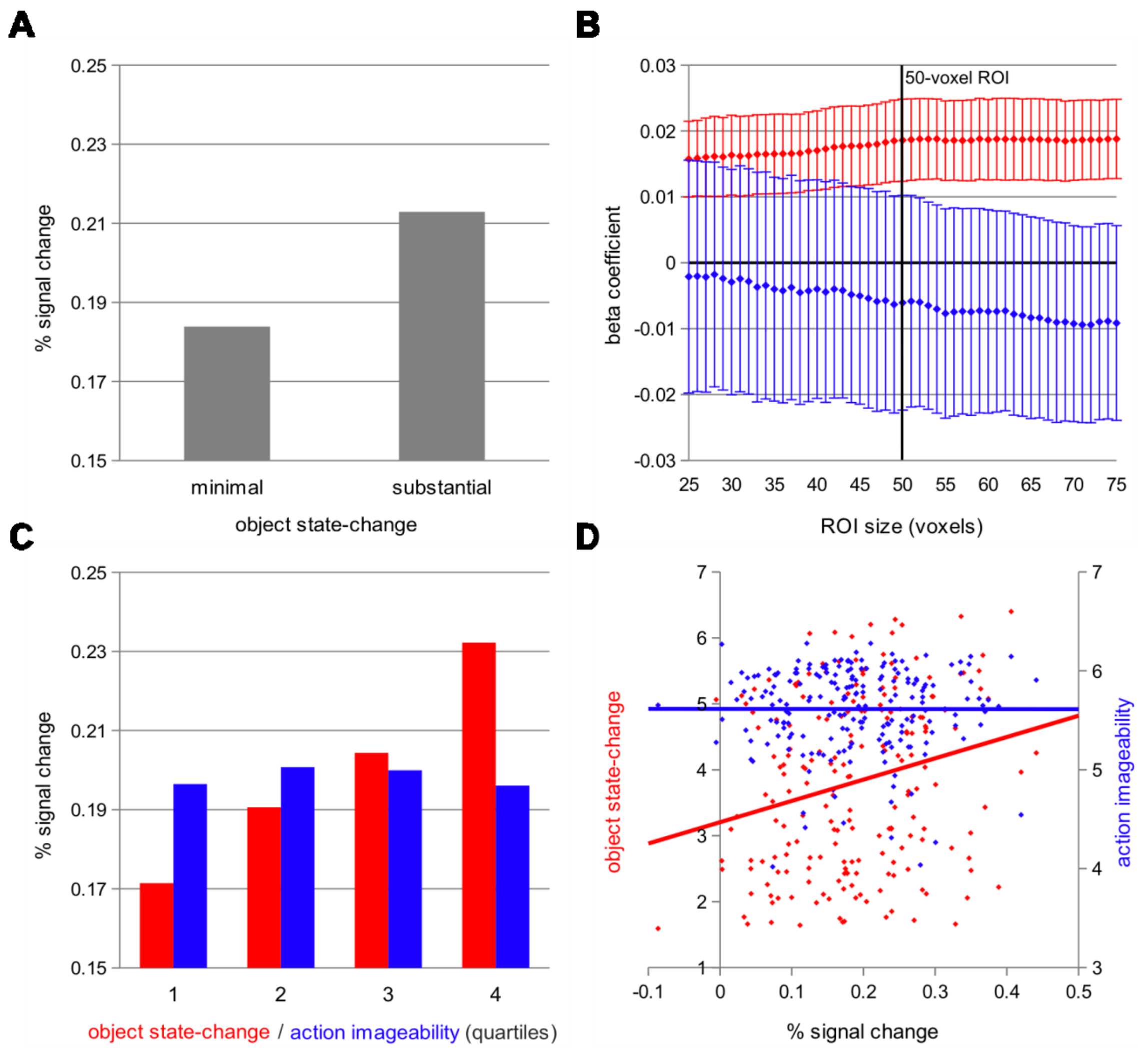

Figure 2.4. Experiment 2 left pVLPFC Stroop-conflict ROI analysis. (A) Categorical analysis. (B) Subject-wise parametric analysis beta coefficients across a broad range of ROI sizes. (C) Binned quartile visualizations of the subject-wise parametric analysis. (D) Item analysis of stimulus ratings and voxel activation.

Though the same verb was used across conditions in the first sentence of each Experiment 2 item, individual verbs may have multiple action connotations. To control for the potential variability of action connotation, a large subset of the Experiment 2 stimuli (60 of the 100 total items) were matched as nearly as possible on the specific action connotation of the first-sentence verb. In the item-level analysis, the pattern of results in the left pVLPFC Stroop-conflict ROI for this subset of the stimuli was identical to that of the full Experiment 2 stimulus set of 100 items for object state-change ($r(58) = .27$, $p < .001$), and for action imageability ($r(58) = .00$, $p =. 99$).

Comparisons across ROIs

As is evident in Figure 2A, the group-level analysis of the Stroop color-word interference task revealed a separate cluster of conflict-responsive voxels outside of left pVLPFC, in left MFG. Likewise, brain areas other than left pVLPFC, including left MTG, were generally active during sentence reading. We analyzed data from the left MTG region in particular, because of its putative involvement in semantic memory (cf. Martin, 2007)). To examine task-related effects in conflict-responsive MFG regions and language-responsive MTG regions, we identified for each subject the 50 left MFG voxels with the highest *t*-statistics in a contrast of conflict trials versus neutral trials in the Stroop task, and the 50 left MTG voxels with the highest *t*-statistics in a contrast of all event comprehension trials (averaged across conditions) versus baseline (Figure 5A). As was the case in left pVLPFC, the location of the top 50 conflict-responsive voxels in left

MFG, and the top 50 language-responsive voxels in left MTG, varied widely across subjects (Figure 5A).

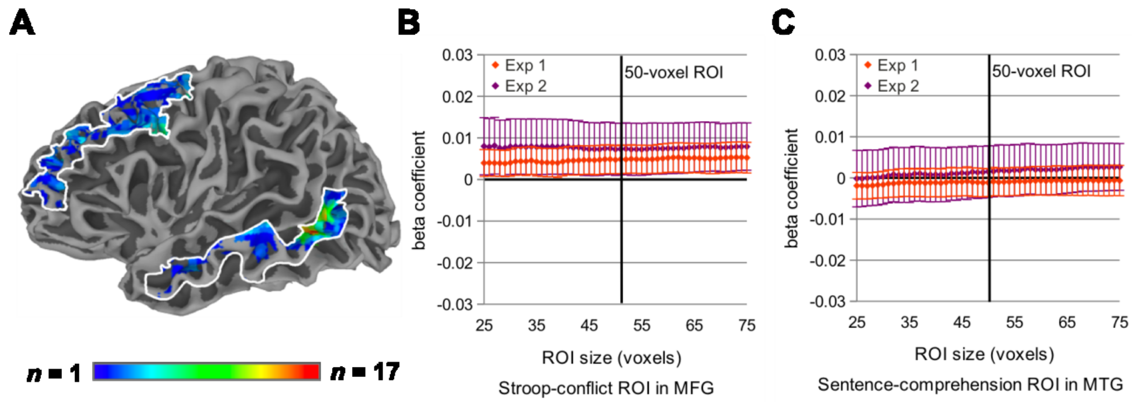

Figure 2.5. Left MFG and left MTG ROI analysis for Experiments 1 and 2. (A) Probabilistic overlap maps of the subject-specific Stroop-conflict ROI in left MFG and the subject-specific sentence-comprehension ROI in left MTG. (B) Subject-wise parametric analysis beta coefficients across a broad range of Stroop-conflict ROI sizes for each experiment in left MFG. (C) Subject-wise beta coefficients across a broad range of sentence-comprehension ROI sizes for each experiment in left MTG.

Unlike the pVLPFC region described earlier, these two control regions each responded to only one of our two functional localizers: The Stroop-conflict ROI in left MFG was not on average responsive during sentence reading, while the sentence-comprehension ROI in left MTG was not responsive to Stroop conflict. The average left MFG signal change across all sentential conditions was not reliably different from baseline in either Experiment 1 ($t(15) = -0.02$, $p = .98$) or Experiment 2 ($t(15) = -1.10$, $p = .29$). Likewise, left MTG signal change was not reliably different between Stroop conflict trials and neutral trials in either Experiment 1 ($t(15) = 0.55$, $p = .59$) or Experiment 2 ($t(15) = -1.29$, $p = .22$). Within these subject-specific ROIs, we repeated for each experiment the subject-wise and item-wise analyses described above for object state-change and action imageability.

For each experiment, we used an ANOVA to test for the interaction between region (pVLPFC, MFG, and MTG) and the degree to which the object state-change ratings predicted BOLD response amplitude. Object state-change beta coefficients differed significantly across ROIs for both Experiment 1 ($F(2,30) = 3.98$, $p = .03$) and Experiment 2 ($F(2,30) = 3.74$, $p = .04$). Planned comparisons further revealed that object state-change did not reliably predict signal amplitude in either the left MFG Stroop-conflict ROI (Figure 5B) or the left MTG sentence-comprehension ROI (Figure 5C). For Experiment 1, beta coefficients for object state-change were reliably different between left MTG and left pVLPFC ROIs ($t(15) = 3.43$, $p = .004$), while the difference between left MFG and left pVLPFC beta coefficients did not reach significance ($t(15) = 1.17$, $p = .26$). For Experiment 2, object state-change beta coefficients in both left MTG ($t(15) = 2.36$, $p = .03$) and left MFG ($t(15) = 2.44$, $p = .03$) were reliably different from pVLPFC. Object state-change beta coefficients were not reliably different between left MTG and left MFG in either experiment (p's > .1).

We conducted a similar set of analyses in order to examine interactions between region and imageability. The action imageability beta coefficients did not reliably differ across ROIs for either Experiment 1 ($F(2,30) = 1.97$, $p = .16$) or Experiment 2 ($F(2,30) = 1.31$, $p = .28$). Experiment 1 planned comparisons, however, revealed a negative correlation between action imageability ratings and left MTG response amplitude ($t(15) = -2.2$, $p = .04$), while the difference between action imageability beta coefficients in left MTG and left pVLPFC was marginally reliable ($t(15) = 1.77$, $p = .10$). In Experiment 2, in which the variance of the action imageability ratings was more constrained ($\sigma2$ = 0.37 for Experiment 1; $\sigma2$ = 0.18 for Experiment 2), MTG beta coefficients for action imageability did not reliably differ either from baseline or from any other ROI (*p*'s > .1).

Whole-brain conjunction analysis of Experiments 1 and 2

To compare the influence of object state-change on neural activity across the two experiments, we first co-varied out activation predicted by the action imageability ratings for each experiment, and then measured the extent to which activation of each voxel was predicted by the object state-change ratings (correcting for multiple comparisons). Both experiments showed extensive change-related activity in left pVLPFC (Figure 6A; Table 2.2). Additionally, there was an interaction between Experiment and the object state-change effect in the right inferior parietal lobule, an area specifically implicated in studies of gesture recognition and body schema, in which action understanding is independent of objects (Hermsdörfer et al., 2001; Chaminade, Meltzoff, & Decety, 2005). Right supramarginal gyrus was significantly more responsive to object state-change in Experiment 1, in which the described action varied across "substantial state-change" and "minimal state-change" conditions, than in Experiment 2, in which the described action was identical across conditions (Figure 6B).

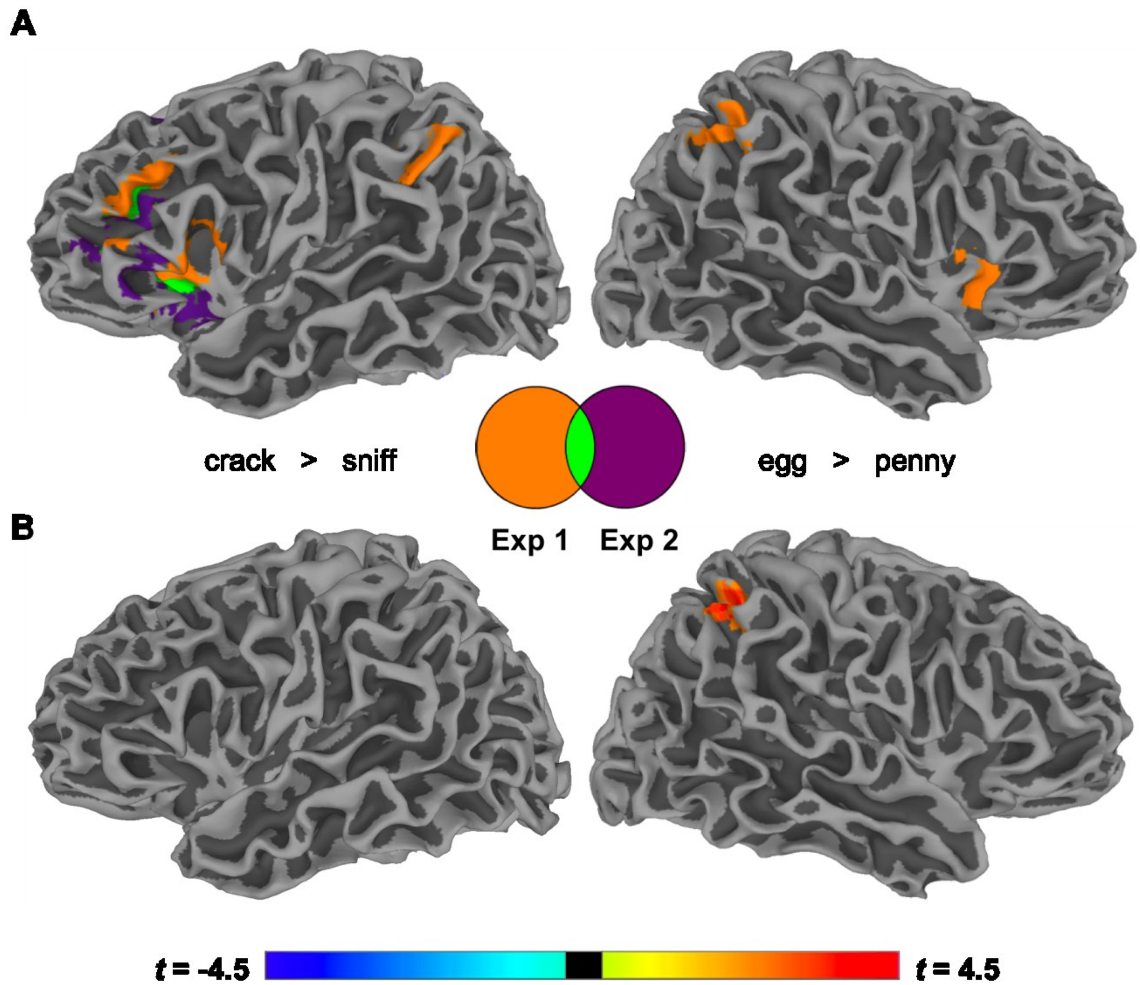

Figure 2.6. Whole-brain conjunction analysis of Experiments 1 and 2. (A) Overlap of Experiment 1 and Experiment 2 voxels reliably predicted by the object state-change ratings, after removing variance predicted by the action imageability ratings. (B) Between-experiment differences in object state-change responsive voxels. Each contrast is thresholded at $p < .05$, corrected for multiple comparisons.

Experiment 1 (object fixed, action varied)

# vox	*peak t*	*x*	*y*	*z*	*Brain region*
182	6.7	43.5	-10.5	11.5	L. pVLPFC (p. opercularis)
143	7.42	-46.5	55.5	47.5	R. supramarginal gyrus
109	5.91	40.5	-25.5	29.5	L. pVLPFC (inferior frontal sulcus)
105	5.53	40.5	43.5	35.5	L. supramarginal gyrus
74	4.45	1.5	-19.5	41.5	L. DMPFC
57	4.91	-28.5	-19.5	2.5	R. insula

Experiment 2 (object varied, action fixed)

# vox	*peak t*	*x*	*y*	*z*	*Brain region*
188	6.13	52.5	-28.5	2.5	L. pVLPFC (p. triangularis)
139	5.67	10.5	4.5	20.5	L. caudate nucleus
136	5.81	4.5	-34.5	32.5	L. DMPFC
52	4.05	40.5	-40.5	11.5	L. pVLPFC (p. triangularis)

Experiment 1 > Experiment 2

# vox	*peak t*	*x*	*y*	*z*	*Brain region*
79	4.31	-46.5	43.5	41.5	R. supramarginal gyrus

Table 2.2. Whole-brain analysis for Experiments 1 and 2. Clusters of voxels reliably predicted by the object state-change ratings, after removing variance predicted by the action imageability ratings. Each contrast is thresholded at of p < .05, corrected for multiple comparisons. There were no statistically reliable voxel clusters with Experiment 2 > Experiment 1. Talairach coordinates and anatomical labels indicate the location of the peak voxel of each cluster. DMPFC = dorsomedial prefrontal cortex.

Discussion

Tracking objects across events requires maintaining multiple representations of the same object in different states. We demonstrate that this component of event cognition elicits a neural response in left pVLPFC that overlaps with increased activation for conflict trials in a Stroop color-word interference task. Through analysis of rated stimulus norms, we further observe that the degree to which an object is changed during an event parametrically predicts the BOLD response amplitude in left pVLPFC voxels most sensitive to Stroop conflict; the rated imageability of the action does not. In Experiment 1, the described object was identical for the "substantial state-change" and "minimal state-change" conditions; the state-change manipulation was thus driven by the described action. In Experiment 2, the described action was identical across conditions; this state-change manipulation was driven instead by the affordances of the described object.

Convergence across experiments demonstrates the generalizability of the effects of object state-change on semantic conflict. By varying the number of voxels included in the left pVLPFC Stroop-conflict ROI, we demonstrate that this effect is robust within subjects across a wide range of ROI sizes. Moreover, the reliable item-wise correlations between object state-change ratings and BOLD response amplitude in the left pVLPFC Stroop-conflict ROI suggest that the effects generalize across a diverse stimulus population of actions, objects, and events, and highlights the utility of item analysis of fMRI data (Bedny et al., 2007).

In each experiment we observe a dissociation among three sets of voxels: 1) voxels in left pVLPFC that are sensitive to Stroop conflict and are activated above baseline during sentence comprehension, 2) voxels in left MFG that are sensitive to Stroop conflict but are *not* activated above baseline during sentence comprehension, and 3) voxels in left MTG that are *not* sensitive to Stroop conflict but are activated above baseline during sentence comprehension. In each experiment, object state-change ratings parametrically predicted BOLD amplitude in the left pVLPFC Stroop-conflict ROI, while action imageability ratings did not. This functional dissociation within the left pVLPFC

Stroop-conflict ROI is in stark contrast to patterns of results in both left MFG and left MTG.

In the left MFG Stroop-conflict ROI, which was responsive to Stroop conflict but not to sentence reading, neither object state-change nor action imageability reliably predicted BOLD amplitude. While left MFG has been shown to be responsive to Stroop conflict beyond the level of motor response (Milham et al., 2001), it is generally not associated with *semantic* conflict (Binder et al., 2009), and dissociates from left pVLPFC with respect to item-specific memory interference, as evidenced by neuroimaging (D'Esposito et al., 1999), patient lesion (Thompson-Schill et al., 2002), and transcranial magnetic stimulation (Feredoes & Postle, 2010) studies. Instead, posterior-most areas of left MFG, where we observe the greatest cross-subject overlap of this ROI, may be specifically involved in maintaining *task* representations (Derrfuss, Brass, Neumann, & Von Cramon, 2005).

In the left MTG sentence-comprehension ROI, which was not responsive to Stroop conflict but was responsive during sentence reading, object state-change did not predict BOLD amplitude in either experiment. However, in Experiment 1, the rated imageability of the described action negatively correlated with MTG signal. Because event comprehension places a stronger demand on semantic retrieval processes when it is more difficult to bring to mind a clear mental image of the described action, the negative correlation of action imageability ratings with left MTG activation is concordant with studies of left MTG responsiveness to difficulty manipulations in semantic retrieval tasks (e.g., Whitney, Kirk, O'Sullivan, Lambon Ralph, & Jefferies, 2011). The absence of an action imageability effect in Experiment 2 is predicted by reduced variance of the action imageability ratings (the described action was fixed across state-change conditions). The modulation of left pVLPFC and left MTG response by object state-change and action imageability respectively, replicates previous dissociations between these regions (e.g., Thompson-Schill, D'Esposito, & Kan, 1999; M. Bedny et al., 2008), indicating functionally distinct contributions of these regions to event comprehension.

In contrast to left MTG and left MFG, left pVLPFC is consistently shown to be central in resolving competition amongst incompatible semantic representations (Thompson-Schill, Bedny, & Goldberg, 2005). Neuroimaging, patient lesion, and transcranial magnetic stimulation studies demonstrate that left pVLPFC is activated during and is necessary for overriding misinterpretations of syntactically ambiguous sentences (January et al., 2009), selecting context-appropriate meanings of ambiguous words (Metzler, 2001; Hindy, Hamilton, Houghtling, Coslett, & Thompson-Schill, 2009), completing sentences that have multiple alternative responses (Robinson et al., 1998; Robinson et al., 2005), generating verbs with many semantic competitors (Thompson-Schill et al., 1997), and resolving working memory interference in item recognition (Feredoes et al., 2006; Feredoes & Postle, 2010).

Stepping back from the ROIs, and examining activation across the entire brain, we see that voxels sensitive to the object state-change manipulation overlapped across experiments in left pVLPFC. In contrast, areas of the inferior parietal lobe that were sensitive to the state-change manipulation in Experiment 1 were not sensitive to this manipulation in Experiment 2. Because the described action varied across conditions in Experiment 1, but was fixed across conditions in Experiment 2, this dissociation is consistent with literature that associates these inferior parietal lobe areas with action representation independent of the objects acted upon (Glover, 2004).

Stepping back further, and considering the theoretical implications of these data, correlations between rated degree of object state-change and BOLD response in the left pVLPFC Stroop-conflict ROI may at first seem consistent with an account that the more an object is changed in state during the first sentence of a trial, the more information must be inferred to derive the context-appropriate representation of the same object in the second sentence. This would predict, however, an interaction with temporal context in Experiment 1, because in the 'and then' case, the state computed at the end of the first sentence is identical to that referred to at the end of the second (but would be different in the 'but first' case). There was no such interaction. Additionally, Experiment 2 subjects only ever read "*and then"* versions of the stimuli, encouraging maintenance of only the changed instantiation, yet we still observed evidence of conflict. Alternatively, one might suppose that the more an object is changed in state, the more information must be kept in memory. This would not predict any interaction with temporal context. However, the left pVLPFC has elsewhere been shown to be associated with resolving interference in working memory *independently* of working memory itself (Thompson-Schill et al., 2002). Thus, the location in which we observe sensitivity to object state-change, as well as the functional specificity of the ROI to Stroop conflict, suggests that our data do not reflect memory load.

We conjecture instead that multiple instantiations of the same object (whether of the object representation in its entirety, or of components of the object representation) must be represented when the object is described as changing in state, and that there is interference between these instantiations. This could include interference between the sensorimotor instantiations of the different affordances associated with distinct object states, mediated by the event representations within which multiple object instantiations are distinguished (cf. Zwaan & Radvansky, 1998). Because objects were generally changed from a canonical state to a marked state, the strength of the initially activated object representation may modulate the extent to which this initial representation remains active even after the contextually appropriate object representation has been computed. And while language and memory research (Bower, 2000; Van Dyke & McElree, 2006) has shown evidence of *similarity*-based interference between actively maintained object representations, we find that the more *dissimilar* the 'before' and 'after' instantiations of an object, the greater the interference. This difference between distinct *objects* (similarity-based interference) and distinct *instantiations* of a single object (dissimilarity-based interference) may have its roots in the fact that the distinct instantiations of an object across event-time (i.e., the 'before' and 'after') are mutually exclusive—they cannot co-exist. Distinct *objects*, on the other hand, can co-exist no matter how similar; the greater the overlap between the objects' representations, the greater the interference, but differences between the objects do not have consequences for co-existence and are not inhibitory. When we need to categorize distinct representations as instantiations of a single object, left pVLPFC may act as a top-down modulatory signal to bias candidate representations—and the neural patterns that instantiate them—toward the context-appropriate representation of the object, performing a similar interference resolution process as described for other forms of ambiguity resolution (Thompson-Schill & Botvinick, 2006).

Our ability to comprehend, represent, recall, and narrate events is a quintessentially human ability. Yet the representation of multiple instantiations of the same object across "event time" (i.e., before, during, and after the event occurs), and how these may compete with one another, is a topic that has not received attention in cognitive psychology. Taken together, data reported here suggest that the need to represent the same object in different states comes at a competitive *cost.* The work reported here is a step toward identifying these representational mechanisms, and speaks to future cognitive models of object and event representation, allowing more detailed exploration of the representations over which the human cognitive system operates.

CHAPTER 3: DISTRIBUTED NEURAL SIMILARITY OF OBJECT STATES PREDICTS PREFRONTAL CONFLICT RESPONSE

> The sense of our meaning is an entirely peculiar element of the thought . . . whose neural counterpart is undoubtedly a lot of dawning and dying processes too faint and complex to be traced.
>
> – *The Principles of Psychology* (William James, 1890)

Abstract

Prefrontal cortex is thought to exert executive control over posterior brain regions that store and maintain information. Previous work demonstrates that comprehension of an object state-change involves interference between incompatible representations of the same object, and evokes a neural response in prefrontal cortex that is the same as for other forms of conflict. Using fMRI and multivariate pattern analysis, we find that the physical similarity of incompatible object states before and after a described event predicts both the strength of the conflict response in left ventrolateral prefrontal cortex, as well as the multivariate pattern-similarity of the corresponding brain states in early ventral visual cortex. Moreover, visual cortex multivariate pattern-similarity predicts the strength of the prefrontal cortex conflict response even better than the rated similarity of the object states. Results suggest that alternative states of an object correspond to distinct visual cortex representations, and that conflict measured in prefrontal cortex is mediated by the similarity of distributed representations in visual cortex.

Introduction

Tracking multiple representations of the same object as it undergoes a state-change engenders conflict due to the need to distinguish the ‘before’ and ‘after’ states of the object. This source of conflict is suggested by recent eye-tracking and neuroimaging studies, which also reveal that this conflict evokes a neural response in left posterior ventrolateral prefrontal cortex (pVLPFC) that is the same as for other known forms of conflict (Altmann & Kamide, 2009; Hindy, Altmann, Kalenik, & Thompson-Schill, 2012). This left pVLPFC conflict response suggests that the internal representations of alternative object states may be incompatible and distinct from one another. We hypothesize that the degree to which internal representations of object states are in fact distinct will be reflected in the similarity between distributed patterns of neural activation that underlie object-specific brain states.

Using functional magnetic resonance imaging (fMRI) and a combination of multivariate and univariate data analysis, we test (1) whether comprehension of an object state-change causes a distinct distributed pattern of the BOLD response in ventral visual cortex (VVC) as well as left pVLPFC, (2) whether comprehension of an object state-change causes a univariate amplitude-modulation of the average BOLD response in VVC and in left pVLPFC, and (3) whether there is a predictive relationship between multivariate pattern-similarity in VVC and univariate amplitude-modulation in left pVLPFC. Through an initial multivariate pattern-similarity searchlight analysis (Kriegeskorte, Goebel, & Bandettini, 2006), we identified subregions of VVC for which object state-change best predicted multivariate pattern-similarity, and measured the extent to which these VVC subregions overlapped with areas of VVC that were most responsive to either feature-scrambled objects or intact objects (Kourtzi & Kanwisher, 2001; Grill-Spector & Malach, 2004). For a subsequent ROI analysis, we identified separately for each subject the feature-sensitive (early visual) and object-sensitive (late visual) visual areas, and areas of left pVLPFC most responsive to conflict trials in a Stroop color-word interference task (Milham et al., 2001; Liu, Banich, Jacobson, & Tanabe, 2006). Within each ROI, we measured multivariate pattern-similarity (Pearson correlation) and univariate amplitude-modulation (difference in the average BOLD response amplitude) across within-trial time points of an fMRI variant of a traditional pretest-posttest experimental design.

Direct comparison of object-specific brain states before and after a described action was afforded by a pre-action/post-action fMRI design. Each experiment trial began with a briefly presented object photograph, followed by a sequence of three visual imagery task instructions separated by fixation: imagine the object, then imagine a specified action involving the object, and finally imagine the object in its final state after the action. Across trials, we varied whether a described action minimally changed the depicted object (e.g., "pick up the balloon"; Figure 3.1A), or substantially changed the object (e.g., "inflate the balloon"; Figure 3.1B). To compare subjects' brain states before and after the object state-change, we separately modeled the BOLD response for each trial component before comparing the multivariate pattern-similarity and the univariate amplitude-modulation across the pre-action and post-action time points (Figure 3.2).

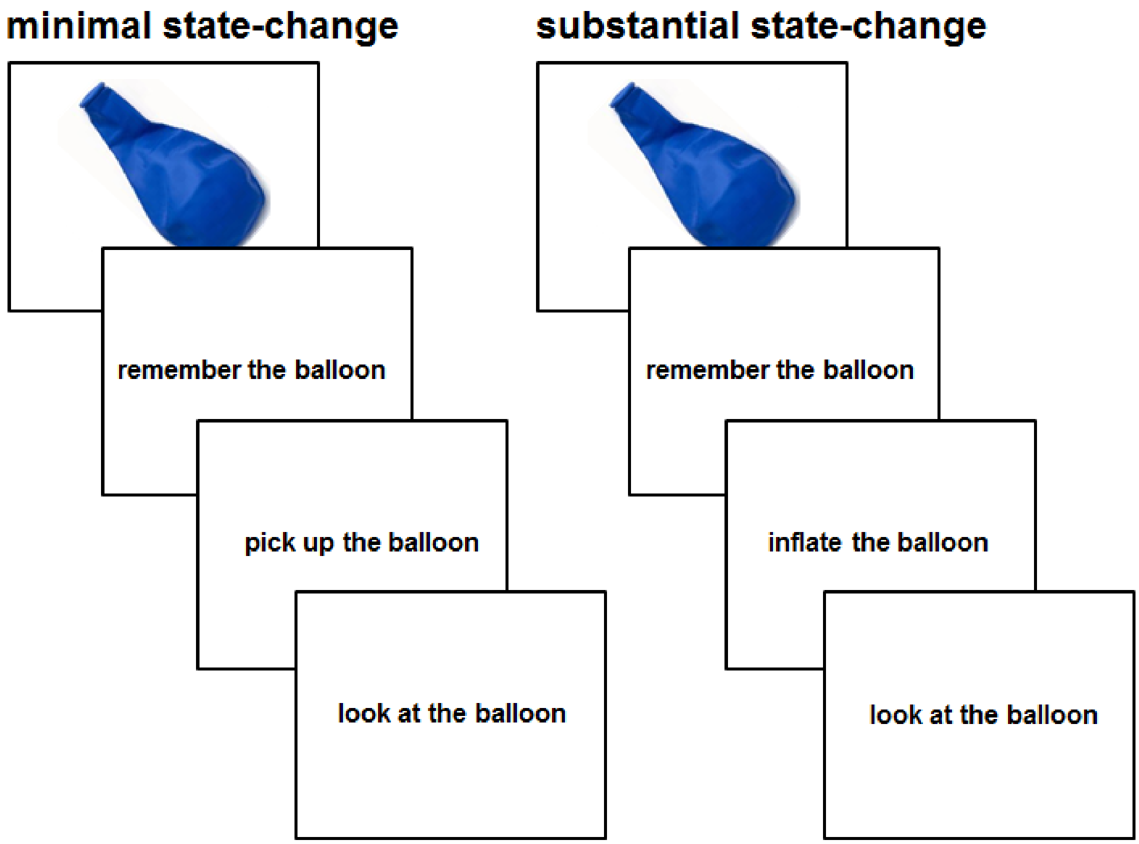

Figure 3.1. Pre-action/post-action fMRI design. Each experiment trial began with a briefly presented object photograph, followed by a sequence of three visual imagery task instructions separated by fixation: imagine the object, then imagine a specified action involving the object, and finally imagine the object in its final state after the action. Subsequent to the three visual imagery segments, a retrieval cue instructed subjects to indicate which of two clipart images is most similar to the object at either the beginning or end of the trial. One of the clipart images depicted the object in its original state, while the other clipart image depicted the object in the altered state that resulted in the substantial state-change condition. Each slide was four seconds in duration, with six seconds of fixation between slides. The BOLD response was separately modeled for each trial component.

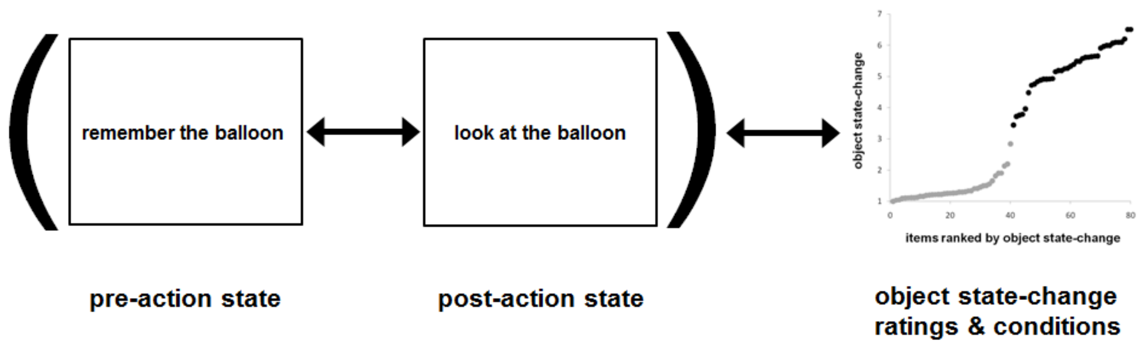

Figure 3.2. Pattern-similarity and amplitude-modulation measurements. To examine the effects of object state-change on across-time multivariate pattern-similarity and univariate amplitude-modulation, we separately modeled the BOLD response for each trial component, and compared the time point in which subject imagined the initial state of the object (pre-action state) to the time point in which subjects imagined the end state of the object (post-action state). Plot on the far right shows the object state-change rating for each item in the state-change comprehension task, ranked by object state-change, and color-coded according to condition (i.e., "minimal state-change" or "substantial state-change").

Results

Behavioral Data

Subjects correctly identified the indicated object on the subsequent-retrieval slide for 87.0% (*SD* = 8.1%) of minimal state-change trials, and 94.6% (*SD* = 5.7%) of substantial state-change trials ($t(13) = 2.68$, $p = .02$). Overall high accuracy on the subsequent-retrieval task indicates consistent attention to the task throughout the scan. Slightly lower accuracy for the minimal state-change trials than for the substantial state-change trials is not surprising given that subjects were never exposed to the alternative object state for minimal state-change trials, thus making the clipart images less distinguishable from one another. On the Stroop color-word interference task, subjects correctly answered 98.3% (*SD* = 2.4%) of all trials. The average response time was 790 ms (*SD* = 165 ms) for conflict trials and 755 ms (*SD* = 184 ms) for neutral trials ($t(13) = 2.64$, $p = .02$). For the perceptual localizer, in which subjects performed a one-back repeated-image detection task, subjects correctly identified 79.3% (*SD* = 24.6%) of repeated intact objects, and 72.1% (*SD* = 26.9%) of repeated feature-scrambled objects ($t(13) = 2.54$, $p = .02$). Lower detection accuracy for feature-scrambled repeats than for intact-object repeats may indicate a difference between conditions regarding the perceptual difficulty of the detection task.

Multivariate Pattern-Similarity Searchlight Analysis

We used a multivariate searchlight analysis (Kriegeskorte, Goebel, & Bandettini, 2006) to examine the effect of object state-change on the visual cortex multivariate pattern-similarity between time points before and after the imagined action. We constrained searchlight analyses to bilateral VVC, which included inferior occipital cortex, lingual gyrus, and the posterior aspects of fusiform gyrus and inferior temporal gyrus. We passed a three-dimensional searchlight with a 3-voxel radius over every voxel within this VVC mask. Unless constrained by a boundary on the outermost edge of the VVC mask, each spherical searchlight comprised 123 voxels. Within each searchlight, we made three separate comparisons for each subject, and assigned the resulting measurements to the central voxel of the searchlight. The first comparison was univariate, and based on a perceptual localizer in which subjects viewed alternating 16-second blocks of intact and feature-scrambled objects. In this perceptual localizer, we measured the relative amplitude of the BOLD response at time points when subjects were viewing either intact or feature-scrambled objects. The second two comparisons were multivariate and based on data from the state-change comprehension task. For each of the multivariate analyses, we measured the Pearson correlation between time points in which subjects imagined each object in its initial form, and then imagined the same object in its new form after a minimal or substantial state-change action. Once these pre-action/post-action similarity scores were computed, we measured the extent to which this similarity score could be predicted by either state-change rating (continuous searchlight analysis) or state-change condition (categorical searchlight analysis).

Continuous Multivariate Searchlight Analysis

For the continuous multivariate searchlight analysis, we used the data from ratings of object state-change to examine the extent to which pre-action/post-action multivariate pattern-similarity varied in proportion to the rated degree of object state-change. The 250 searchlight spheres for which pre-action/post-action multivariate pattern-similarity most negatively correlated with the rated object state-change of the items are plotted in yellow in Figure 3.3A. As is evident in Figure 3.3A, the 250 searchlights for which the object state-change ratings best predicted multivariate pattern-similarity were almost exclusively in lingual and inferior occipital gyri. Moreover, these ratings-predicted searchlights overlapped extensively (105 of the 250 searchlights) with the feature localizer (colored in blue in Figure 3.3), and did not overlap at all with the object localizer (colored in red).

Categorical Multivariate Searchlight Analysis

For the categorical searchlight analysis, we split each subject’s dataset into minimal state-change and substantial state-change conditions, and computed the average pre-action/post-action similarity across all items in each condition. This resulted in two statistical maps of VVC for each subject: one statistical map that reflected the average pre-action/post-action multi-voxel similarity for the minimal state-change condition, and one statistical map that reflected the average pre-action/post-action multi-voxel similarity for the substantial state-change condition. These statistical maps were compared across all subjects using repeated-measures *t*-tests that measured the reliability of pre-action/post-action similarity differences between substantial state-change and minimal state-change conditions for each VVC searchlight. As in the continuous multivariate searchlight analysis, searchlight spheres that were most sensitive to object state-change when treated as a categorical variable tended to be in lingual and inferior occipital gyri, and overlapped exclusively with the feature localizer (130 of the 250 searchlights; Figure 3.3B).

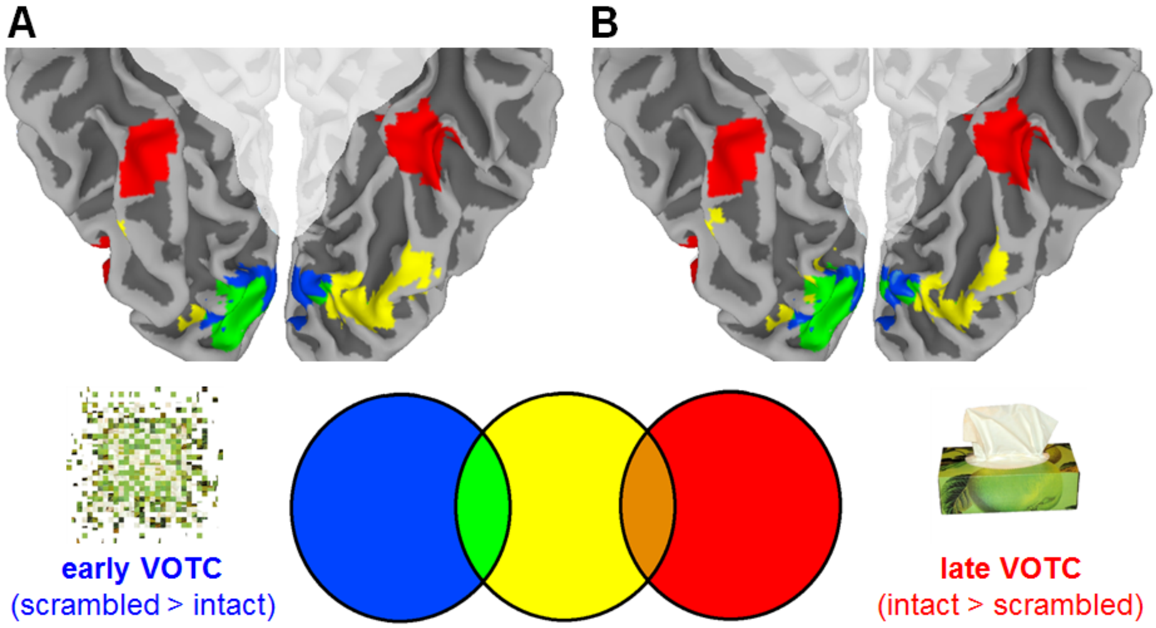

Figure 3.3. Multivariate pattern-similarity searchlight analysis. (A) Overlap of the visual cortex functional localizers and the 250 most reliable VVC searchlights in which similarity across time points negatively correlated with the degree of object state-change (continuous multivariate searchlight analysis). (B) Overlap of the visual cortex functional localizers and the 250 most reliable VVC searchlights in which patterns for the substantial state-change condition were less similar across time points than were patterns for the minimal state-change condition (categorical multivariate searchlight analysis). In both A and B, early visual is in blue, and includes the 250 VVC voxels that were most responsive to feature-scrambled objects in a perceptual localizer. Late visual is in red, and includes the 250 VVC voxels that were most responsive to intact objects in the perceptual localizer. Brain regions that are shaded in white in the images above were not included in the VVC anatomical mask.

ROI Analysis

We examined the effect of object state-change on both the multivariate pattern-similarity and the univariate amplitude-modulation of the BOLD response in three ROIs: early visual cortex, late visual cortex, and left pVLPFC. Each ROI was anatomically constrained and functionally defined on the individual-subject level. Within each subject-specific visual cortex and pVLPFC ROI, we examined the effect of object state-change on the across-time multivariate pattern-similarity and univariate amplitude-modulation during the object comprehension task. For each ROI analysis, we used an ANOVA to test for the interaction across ROIs (early visual, late visual, and left pVLPFC; Figure 3.3) and the degree to which the object state-change ratings predicted either across-time multivariate pattern-similarity or across-time activation difference in the BOLD response.

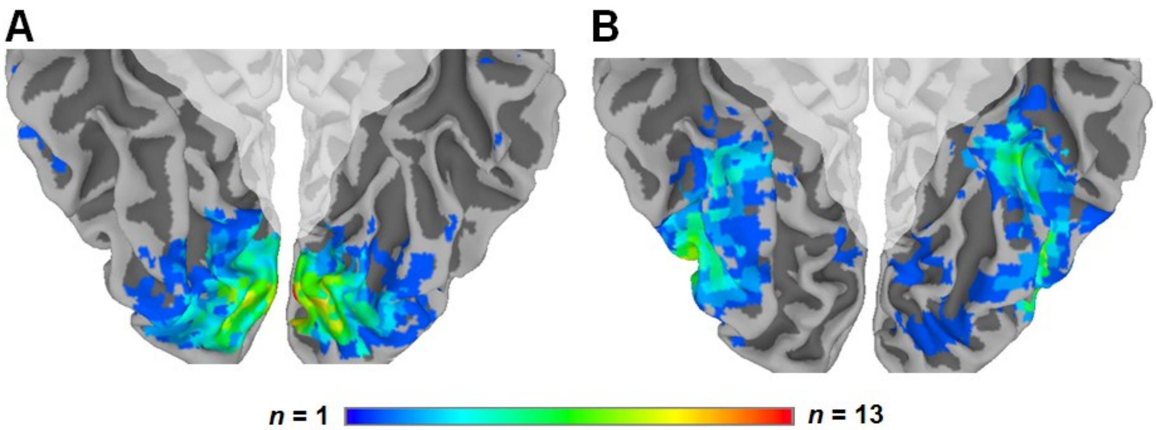

Figure 3.4. Visual cortex ROIs. (A) Frequency overlap map across subjects for the early visual ROI. The early visual ROI was defined separately for each subject as the 250 VVC voxels most responsive to feature-scrambled images compared to intact objects in a perceptual localizer. (B) Frequency overlap across subjects map for the late visual ROI. The late visual ROI was defined as the 250 VVC voxels most responsive to intact objects compared to feature-scrambled objects. The maximum frequency overlap for the early visual ROI was 13/14 subjects, while the maximum frequency overlap for the late visual ROI was 10/14 subjects. Brain regions that are shaded in white in the images above were not included in the VVC anatomical mask.

Visual Cortex ROIs

Functional ROIs for early visual cortex and late visual cortex were defined using a perceptual localizer task in which subjects viewed alternating blocks of intact and feature-scrambled objects while performing a one-back detection task. Late visual cortex was defined as the 250 VVC voxels most responsive to intact objects compared to feature-scrambled objects, while early visual cortex was defined as the 250 VVC voxels most response to feature-scrambled images compared to intact objects. The location of the top 250 object-responsive and feature-responsive voxels was quite stereotyped across subjects, such that object responsive voxels (late visual cortex) tended to be in lateral occipital and fusiform gyri, while feature-responsive voxels (early visual cortex) tended to be in inferior occipital and lingual gyri (Figure 3.4).

Stroop-Conflict ROI in left pVLPFC

Previous studies indicate that left pVLPFC is responsive to conflict at the level of semantic representation, and also that the Stroop color-word interference task is a useful tool to localize conflict-responsive voxels on an individual-subject basis (January et al., 2009; Hindy, Altmann, Kalenik, & Thompson-Schill, 2012). To determine voxels most responsive to conflict on an individual subject level, we identified for each subject the 250 left pVLPFC voxels with the highest t-statistics in a contrast of conflict trials versus neutral trials in a Stroop interference task. In a group-level contrast, left pVLPFC was generally more responsive to Stroop conflict than surrounding cortex (Figure 3.5A), though the location of the top 250 conflict-responsive voxels varied widely across subjects (Figure 3.5B).

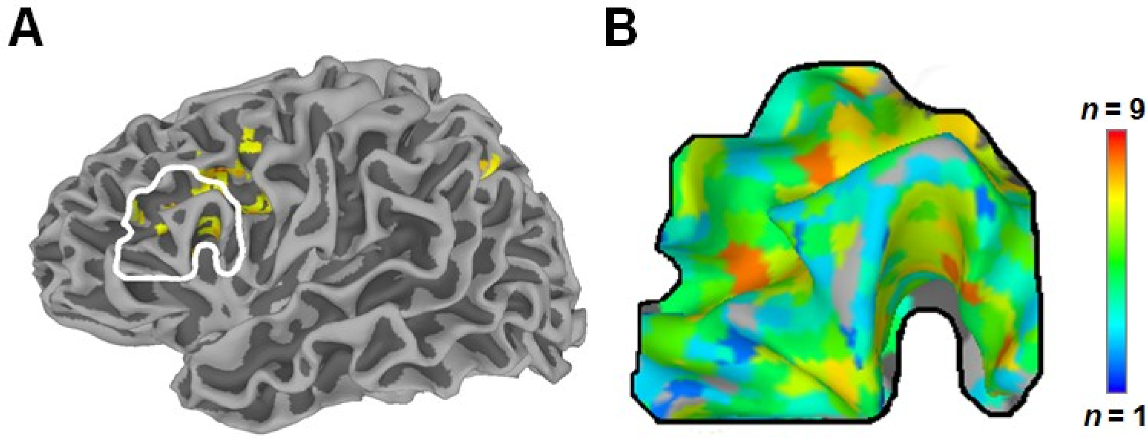

Figure 3.5. Stroop-conflict ROI in left pVLPFC. (A) Whole-brain group-level contrast of conflict trials versus neutral trials in the Stroop color-word interference task, thresholded at a corrected alpha of $p < .01$, and displayed on a partially inflated Talairach surface; left pVLPFC is outlined in white. (B) Frequency overlap map of the subject-specific Stroop-conflict ROI in left pVLPFC. Each subject-specific ROI included the 250 voxels in left pVLPFC with the highest within-subject *t*-statistics for the Stroop contrast. The left pVLPFC voxel that had the greatest overlap across subjects included 9/14 subjects.

Multivariate Pattern-Similarity ROI Analysis

The extent to which object state-change ratings predicted multivariate pattern-similarity reliably varied across the three ROIs ($F(2,26) = 5.92$, $p = .02$; Figure 3.5A). Planned comparisons further revealed that object state-change reliably predicted multivariate pattern-similarity in early visual cortex ($t(13) = -2.36$, $p = .03$), but did not reliably predict multivariate pattern-similarity in either late visual cortex or left pVLPFC (p's $> .1$), with a reliable interaction between early visual cortex and left pVLPFC ($t(13) = 3.57$, $p = .003$). An identical pattern of results was found for the condition-wise similarity analysis: object state-change ratings reliably predicted across-time multivariate pattern-similarity in early visual cortex ($t(13) = -2.19$, $p = .05$), and did not predict multivariate pattern-similarity in either late visual cortex or left pVLPFC (p's > .4; Figure 3.5B).

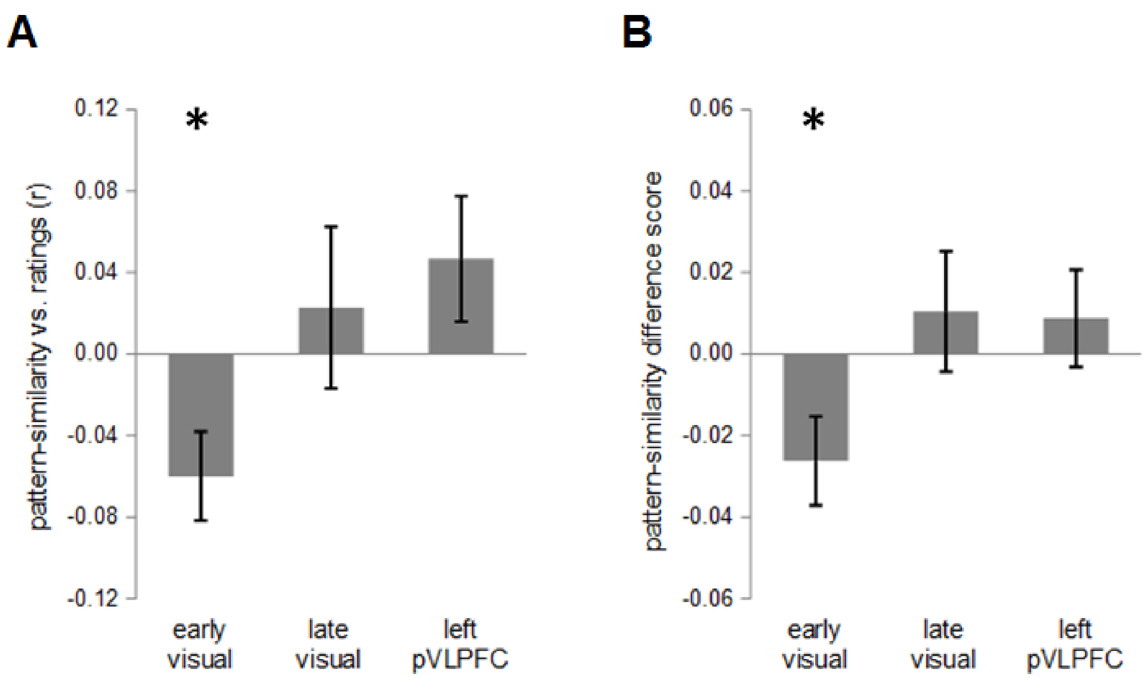

Fig 3.6. Multivariate pattern-similarity ROI analysis. (A) Degree to which object state-change ratings (a continuous variable) predicted pre-action/post-action multivariate pattern-similarity in each ROI. (B) Difference between the substantial state-change and minimal state-change conditions in pre-action/post-action multivariate pattern-similarity for each ROI.

Univariate Amplitude-Modulation ROI Analysis

Continuous object state-change ratings reliably predicted across-time amplitude-modulation in left pVLPFC, such that greater state-change ratings corresponded with greater across-time amplitude differences ($t(13) = 2.27$, $p = .04$; Figure 3.6A). Additionally, the categorical difference between substantial state-change and minimal state-change conditions was reliable in left pVLPFC ($t(13) = 2.62$, $p = .02$). In both early and late visual cortex, there were no univariate amplitude-modulation differences between conditions, and state-change ratings did not reliably predict univariate amplitude-modulation in either visual cortex ROI (p's > .2). Interactions across ROIs in univariate amplitude-modulation did not reach significance (p's > .1).

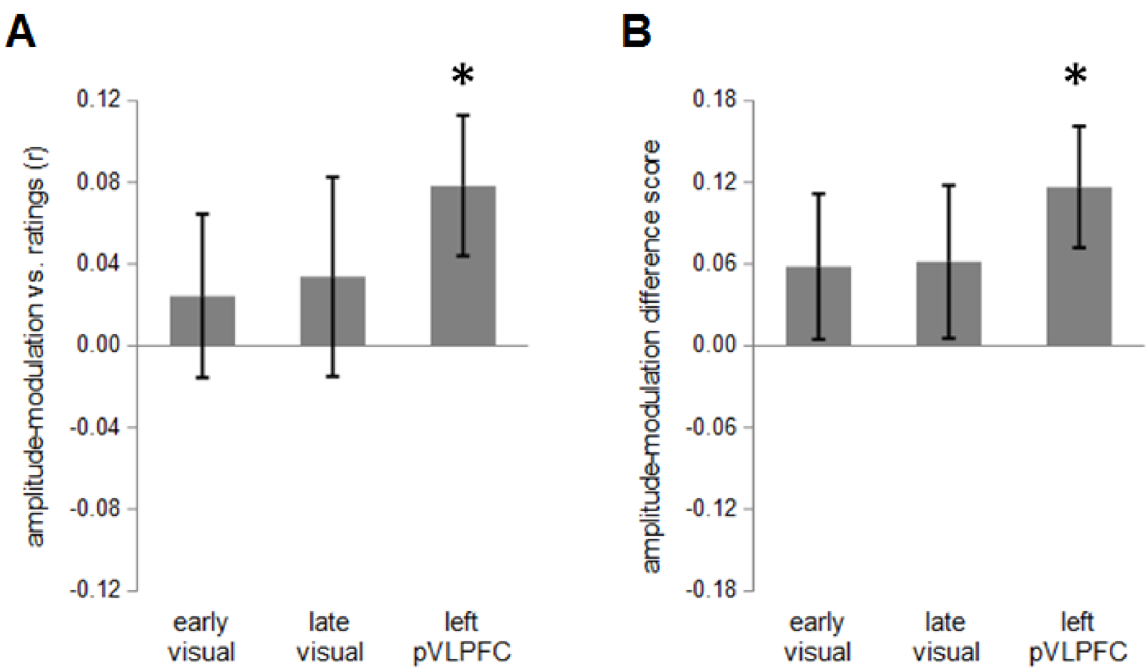

Fig 3.7. Univariate amplitude-modulation ROI analysis. (A) Degree to which object state-change ratings (a categorical variable) predicted pre-action/post-action univariate amplitude-modulation in each ROI. (B) Difference between the substantial state-change and minimal state-change conditions in pre-action/post-action univariate amplitude-modulation for each ROI.

VVC-Predicted Univariate Amplitude-Modulation Analysis

Object state-change ratings and conditions predicted multivariate pattern-similarity in early visual cortex, as well as univariate amplitude-modulation in left pVLPFC. This suggests that multivariate pattern-similarity in early visual cortex may predict univariate amplitude-modulation in left pVLPFC. To test this possibility, we measured for each subject the Pearson correlation between multivariate pattern-similarity in both early and late visual cortex, and univariate amplitude-modulation in left pVLPFC. Pattern-similarity in early visual cortex reliably predicted amplitude-modulation in pVLPFC ($t(13) = -3.35$, $p = .005$; Figure 3.8), while pattern-similarity in late visual cortex failed to reliably predict pVLPFC amplitude-modulation ($t(13) = -1.42$, $p = .18$). Moreover, though not reliably different ($t(13) = -1.14$, $p = .28$), the statistical relationship between early visual multivariate pattern-similarity and left pVLPFC amplitude-modulation ($p = .005$) appears to be *even stronger* than the relationship between the object state-change ratings and pVLPFC amplitude-modulation ($p = .03$).

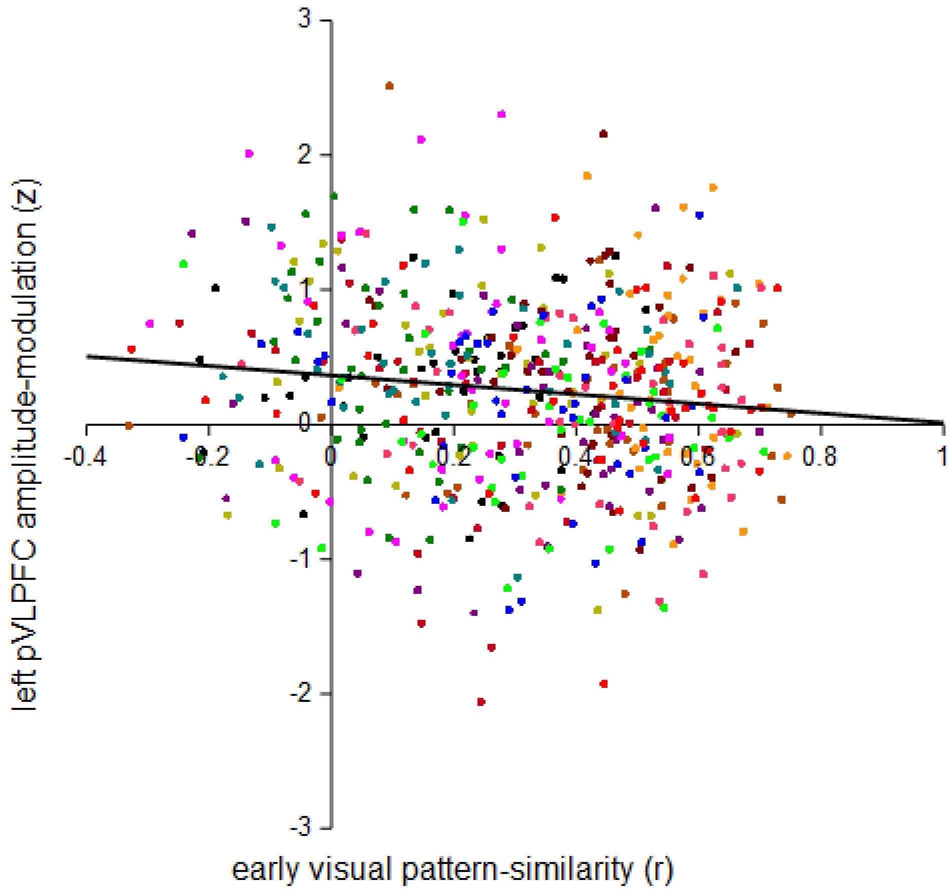

Figure 3.8. VVC-predicted univariate amplitude-modulation of pVLPFC. A separate regression model was calculated for each subject to measure the extent to which multivariate pattern-similarity in the early visual ROI predicted univariate amplitude-modulation in the left pVLPFC ROI. Data for each subject is plotted in a single color, and includes all trials for that subject. For 13/14 subjects, univariate amplitude-modulation in left pVLPFC negatively correlated with multivariate pattern-similarity in early visual. The displayed trend line is across data points from all subjects.

To test the anatomical specificity of VVC-predicted univariate amplitude-modulation of left pVLPFC, and also to identify additional cortical region for which pre-action/post-action univariate amplitude-modulation varied with visual cortex pattern-similarity, we conducted a whole-brain functional connectivity analysis. For every voxel in the brain, we measured the correlation between univariate amplitude-modulation of that voxel, and multivariate pattern-similarity in early visual (Figure 3.8B). Multivariate pattern-similarity in early visual cortex reliably predicted univariate amplitude-modulation of voxels in left pVLPFC. The only additional cortical region in which univariate amplitude-modulation scaled with early-visual multivariate pattern-similarity was the left angular gyrus of the parietal lobe (Figure 3.9; Table 3.1).

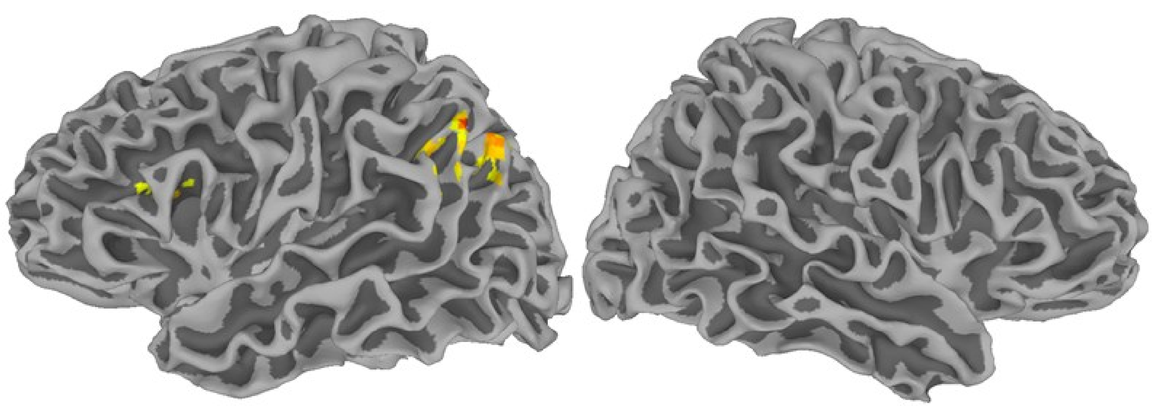

Figure 3.9. Whole-brain VVC-predicted univariate amplitude-modulation. Clusters of voxels for which univariate amplitude-modulation positive correlated with multivariate pattern-similarity in the early visual ROI. This statistical contrast is thresholded at *p* < .01, corrected for multiple comparisons. There were no statistically reliable voxel clusters for which univariate amplitude-modulation positive correlated with early visual multivariate pattern-similarity. Talairach coordinates and anatomical labels indicate the location of the peak voxel of each cluster.

VVC-predicted amplitude-modulation

# vox	*peak t*	*x*	*y*	*z*	*Brain region*
76	-6.26	46.5	58.5	41.5	L. angular gyrus
50	-4.88	49.5	-19.5	23.5	L. pVLPFC (p. triangularis)

Table 3.1. Whole-brain VVC-predicted univariate amplitude-modulation. Clusters of voxels for which univariate amplitude-modulation positive correlated with early visual multivariate pattern-similarity. Contrast is thresholded at $p < .01$, corrected for multiple comparisons. There were no statistically reliable voxel clusters for which univariate amplitude-modulation positive correlated with early visual multivariate pattern-similarity. Talairach coordinates and anatomical labels indicate the location of the peak voxel of each cluster.

Discussion

Prefrontal cortex is thought to exert executive control over more posterior brain regions that store and maintain perceptual information (Miller & Cohen, 2001), and yet cognitive control processes in prefrontal cortex are generally studied independently of perceptual areas (Fuster, 2008). Using a paradigm in which both perceptual similarity and cognitive control demand are precisely manipulated, we simultaneously measured competition between a stimulus-driven visual representation of an object and a cognitive representation of the same object that subjects constructed based on a described action. Through a multivariate pattern-similarity searchlight analysis (Kriegeskorte et al., 2006), we discovered a striking dissociation between early and late areas of VVC. Searchlight spheres that were most sensitive to object state-change tended to be in lingual and inferior occipital gyri, overlapped extensively with voxels that responded more strongly to intact objects than to feature-scrambled objects in a perceptual localizer, and did not overlap at all with voxels that responded more strongly to feature-scrambled objects than to intact objects.

In comparing the pre-action and post-action brain states, we found that multivariate pattern-similarity and univariate amplitude-modulation double-dissociate across three ROIs. In early visual cortex, multivariate pattern-similarity across time points was significantly reduced when an object was substantially changed in state, compared to when the same object was minimally changed. Moreover, multivariate pattern-similarity in early visual cortex varied parametrically with the rated degree to which the object was changed in state by the described action. In late visual cortex as well as left pVLPFC, multivariate pattern-similarity was invariant to both categorical and continuous state-change manipulations. In the ROIs for both early and late visual cortex, the univariate amplitude-modulation across pre-action and post-action object states was nearly identical across conditions, and was not reliably predicted by the object state-change ratings.

Left pVLPFC dissociated from visual areas in both univariate amplitude-modulation and multivariate pattern-similarity. In areas of left pVLPFC that were most sensitive to conflict in a Stroop color-word identification task, the extent of the univariate amplitude-modulation of the BOLD response depended on the degree of object state-change. Left pVLPFC signal amplitude was greater when subjects imagined an object that was substantially different from the immediately preceding photograph, as opposed to when they imagined that object in the same state as in the photograph. This left pVLPFC univariate amplitude-modulation effect replicates a recent study of object state-change during event comprehension (Hindy, Altmann, Kalenik, & Thompson-Schill, 2012), and suggests a specific role for left pVLPFC in representing object state-change that involves similar interference resolution mechanisms as described for verb generation, control of proactive interference (Thompson-Schill et al., 2002; Jonides & Nee, 2006), and resolution of lexical (Rodd et al., 2004; M. Bedny et al., 2008; Hindy et al., 2009) and syntactic (Novick et al., 2005; January et al., 2009) ambiguity. However, multivariate pattern-similarity in left pVLPFC was invariant to the object state-change manipulation. This suggests that neural representations in left pVLPFC are not specific to stimulus features that vary across object states. However, since the task was identical for every item (i.e., focus on the end state of the object), these data are consistent with an active-maintenance model of left pVLPFC in which patterns of neural activation are task-specific, and not item-specific (e.g., Miller & Cohen, 2001; Rougier, Noelle, Braver, Cohen, & O'Reilly, 2005; O'Reilly, Herd, & Pauli, 2010).

Multivariate pattern-similarity in early visual cortex predicted the strength of the conflict response in left pVLPFC even better than separately-collected ratings of the similarity between object states. This predictive relationship between early visual multivariate pattern-similarity and left pVLPFC univariate amplitude-modulation is among the first examples of functional connectivity between distributed representations in posterior brain areas and signal change in frontal cortex. Multivariate pattern-similarity effects in early visual cortex build upon mounting evidence for distributed object representations in VVC (Haxby et al., 2001; Norman, Polyn, Detre, & Haxby, 2006), and informs neural models for the "refreshing" of visual memories (e.g., Johnson, 1992). Previous studies demonstrate that bringing to mind the visual memory of a previously viewed image activates the same areas of visual cortex that were activated during image perception (Johnson, Mitchell, Raye, D'Esposito, & Johnson, 2007; Park, Chun, & Johnson, 2010). Additionally, the act of refreshing an image that was presented just once during encoding enhances repetition attenuation effects to the same extent as having viewed the same image twice during encoding (Yi, Turk-Browne, Chun, & Johnson, 2008). Recent work has shown that competitive remembering is associated both with more ambiguous patterns of VVC reactivation, and with increased activation in prefrontal areas (Kuhl, Rissman, Chun, & Wagner, 2011). The VVC-predicted univariate amplitude-modulation approach introduced here combines similarity-based fMRI analysis of the BOLD response in visual cortex (e.g., Kriegeskorte et al., 2008; Weber et al., 2009) with parametric univariate analysis of the BOLD response in prefrontal cortex (e.g., Hindy et al., 2012).

The anatomical specificity of the VVC-predicted univariate amplitude-modulation to left pVLPFC is remarkable (see Figure 3.9 and Table 3.1). Indeed, the only additional cortical region in which univariate amplitude-modulation scaled with early visual multivariate pattern-similarity was the left angular gyrus of the parietal lobe. Though we did not have an a priori hypothesis about parietal cortex involvement in the state-change comprehension task, numerous neuroimaging, patient deficit, and transcranial magnetic stimulation studies implicate left angular gyrus in the shifting of spatial attention, independent of conflict (e.g., Mort et al., 2003; Wager, Jonides, & Reading, 2004; Chambers, Payne, Stokes, & Mattingley, 2004). In addition to conflict between alternative object representations, it is possible that the substantial state-change items required greater shifts of internal spatial attention. The possibility that the VVP-predicted amplitude-modulation in angular gyrus reflects internal spatial attention processes is particularly noteworthy in the context of recent evidence and discussions of the overlapping neural systems underlying internal and external attention (Kan & Thompson-Schill, 2004; Chun, Golomb, & Turk-Browne, 2011; Carrasco, 2011).

Data presented here informs our understanding of the mnemonic mechanisms that support our ability to juggle representations of mutually exclusive states of the world during event processing. We show that representation of object states involves the interaction of multiple brain areas, including areas of ventral visual processing pathway that are central to visual perception (Ullman, 2000), and areas of prefrontal cortex that are necessary for performance of any task which require cognitive control (Fuster, 2008). VVC-predicted univariate amplitude-modulation effects suggest that left pVLPFC thus appears to exert executive control over posterior brain regions that store and activate information, and that biased competition is an integral part of event cognition, enabling selection of the context-appropriate representation among competing instantiations of the same object as it undergoes change. In this way top-down projections from the prefrontal cortex may bias visual and semantic representations in the retrieval of conceptual knowledge and maintenance of visual imagery. When the comprehender must resolve the interference caused by alternative states of a single object, left pVLPFC may act as a top-down modulatory signal to bias candidate representations (and the neural patterns that instantiate them) toward the context-appropriate representation of the object.

Methods

Subjects

Fourteen right-handed native English speakers (8 female), aged 22-33 years, participated in the study. Subjects were paid $20 per hour and were recruited from within the University of Pennsylvania community. All fMRI subjects gave informed consent as approved by the University of Pennsylvania Institutional Review Board. Additionally, 204 native English speakers participated online in a task used for stimulus norming.

Stimuli

fMRI subjects read 20 items from each of the two conditions. Two counterbalanced lists were created in which each experimental item occurred in only one condition in a list, and across lists every item occurred in all conditions. The only difference between the substantial state-change and minimal state-change conditions was the described action. Each subject saw each item in only one of the two conditions. (See Appendix C for full stimulus set.)

Object state-change ratings for each item were collected through an online survey (N = 106). The 80 total items were randomly split into two lists, with the constraint that each subject rated only one action for each item. For each item, survey subjects were presented with the object photograph and just below the photograph, either the minimal state-change action or the substantial state-change action. Subjects were asked, “Upon the event, will the object stay just the same as it had been before, or will it be changed at all?” Subjects rated each item on a 7-point scale ranging from “just the same” to “completely changed.” The average state-change rating was 5.28 (*SD* = 0.77) for substantial state-change items, and 1.39 (*SD* = 0.77) for minimal state-change items. The difference in rated state-change between the substantial state-change and minimal state-change conditions was reliable ($p < .001$). Figure 3.1 displays the object state-change ratings for each item in the state-change comprehension task, ranked according to its object state-change rating, and color-coded by condition (i.e., “substantial state-change” or “minimal state-change”).

Because we were concerned that conflict effects in left pVLPFC may be influenced by the semantic association between objects and actions (e.g., “inflate” and “balloon” may be more strongly associated than “pick up” and “balloon”), we also collected ratings of the associative strength between each photographed object and described action through a separate online survey (N = 98). As in the state-change survey, subjects viewed each object photograph individually, with either the minimal state-change action or the substantial action printed below the photograph. Subjects were asked, “How strongly is the following action associated with the depicted object?” Subjects rated each item on a 7-point scale ranging from “action not all associated with object” to “action extremely associated with object.” The average association-strength rating was 5.41 (*SD* = 1.10) for substantial state-change items, and 3.23 (*SD* = 0.80) for minimal state-change items. This associative-strength difference between conditions was reliable ($p < .001$). Notably, insofar as minimal state-change actions were less associated with objects than substantial state-change actions, there should be greater conflict for the minimal state-change items than for substantial state-change items. Hypotheses based on the associative strength of objects and actions predict the opposite pattern of results from hypothesis based on the level of object state-change, as well as from those actually observed for the left pVLPFC conflict ROI. That is, object state-change condition predicted univariate amplitude-modulation in the left pVLPFC ROI, *despite* any differences across conditions in the associative of objects and actions. Moreover, associative strength did not reliably predict pVLPFC univariate amplitude-modulation when treated as a continuous variable ($t(13) = 1.00$, $p = .34$).

Procedure

State-Change Comprehension Task

The event comprehension portion of the experiment consisted of 40 trials (20 trials of each condition), separated across five six-minute runs. Each trial lasted six seconds, during which the first sentence was presented for three seconds, followed by the second sentence for three seconds. Subjects pressed the two outer buttons of the keypad when the second sentence was implausible given the first sentence (e.g., "The man will cook the pizza. But first, he will eat the pizza."). Trials were separated by 3 to 15 seconds of jittered fixation, optimized for statistical power by optseq (http://surfer.nmr.mgh.harvard.edu/optseq/). Stimuli for the event comprehension task, as well as for the two functional localizers, were presented using E-Prime (Psychology Software Tools, Pittsburgh, PA).

Stroop Interference Localizer

After the event comprehension runs, subjects performed one run of a Stroop color identification task, based on previously described procedures. The Stroop task was just over 5 minutes in total duration, and the response box was restricted to three buttons:

yellow, green, and blue. Stimuli included four trial types: response-eligible conflict, response-ineligible conflict, and two groups of neutral trials. Subjects were presented with a single word for each trial, and instructed to press the button corresponding to the typeface color of each word. Conflict trials could be either response-eligible or response-ineligible. For response-eligible conflict trials, the color term matched one of the subject's possible responses (i.e., yellow, green, or blue), but always mismatched the typeface color. The color terms for response-ineligible conflict trials (orange, brown, or red) also mismatched the typeface color, but were not possible responses. Separate sets of non-color neutral trials (e.g., farmer, stage, tax) were intermixed with the response-eligible and response-ineligible conflict trials.

Perceptual Localizer

The final run of scanning was a 6-minute functional localizer to identify object-selective regions of interest (ROIs) in lateral occipital and posterior fusiform areas of visual cortex. During the localizer run, subjects viewed intact and feature-scrambled objects while performing a one-back task.

fMRI Image Acquisition

Structural and functional data were collected on a 3-T Siemens Trio system and a 32-channel array head coil. Structural data included axial T1-weighted localizer images with 160 slices and 1mm isotropic voxels (TR = 1620 ms, TE = 3.87 ms, TI = 950 ms). Functional data included echo-planar fMRI performed in 44 axial slices and 3 mm isotropic voxels (TR = 3000 ms, TE = 30 ms). Twelve seconds preceded data acquisition in each functional run to approach steady-state magnetization.

Image Processing & Analysis

Image preprocessing and statistical analyses were performed using AFNI (Cox, 1996) and visualized in SUMA. Functional data were sinc interpolated to correct for slice timing, and aligned to the mean of all functional images using a six parameter iterated least squares procedure. The functional data were then registered with the subject's anatomical dataset, normalized to a standard template in Talairach space, and smoothed with a 4 mm FWHM Gaussian kernel. Finally, all time-series data were *z*-normalized within each run. Each condition was modeled with a canonical hemodynamic response function, and beta coefficients were estimated using a modified general linear model that included a restricted maximum likelihood estimation of the temporal auto-correlation structure, with a polynomial baseline fit and six motion parameters as covariates of no interest.

Regions of interest were defined both anatomically and functionally. Anatomical ROIs were defined in Talairach space using probabilistic cytoarchitectonic probabilistic maps provided in the SPM Anatomy Toolbox (Eickhoff et al., 2005). VVC was anatomically constrained to bilateral ventral occipitotemporal cortex, including included inferior occipital cortex, lingual gyrus, and the posterior aspects of fusiform gyrus and inferior temporal gyrus. Across all subjects, the anatomical definition of VVC included an average of 4059 voxels (SD = 77). Across all subjects, the anatomical definition of VVC included an average of 801 voxels (SD = 33). Within the broad anatomical constraints of bilateral VVC and left pVLPFC, ROIs were functionally defined separately for each subject using the perceptual localizer (blocks of intact and feature-scrambled objects) and the Stroop color-word interference task. The late visual ROI was defined as the 250 VVC voxels most responsive to intact objects compared to feature-scrambled objects, while the early visual ROI was defined as the 250 VVC voxels most response to feature-scrambled images compared to intact objects. Left pVLPFC was anatomically constrained to BA 44 (pars opercularis), BA 45 (pars triangularis), and inferior frontal sulcus. The pVLPFC conflict ROI comprised the 250 voxels with the highest *t*-statistics in a contrast of conflict trials (either response-eligible or response-ineligible) vs. neutral trials during the Stroop interference task. Statistical tests were based either on the mean amplitude difference (univariate amplitude-modulation) or Pearson correlation (multivariate pattern-similarity) across time points of the 250 voxels of each ROI, and were evaluated at the two-tailed .05 level of significance.

CHAPTER 4: GENERAL DISCUSSION

But facts are facts, and if we only get enough of them they are sure to combine.
– *The Principles of Psychology* (William James, 1890)

Event comprehension requires the ability to represent, recall, and imagine individual objects in multiple distinct states. We begin with the observation that physical object state-changes, as they occur in the world, involve distinct and mutually exclusive states of the same object at different times. The experiments described in Chapters 2 and 3 test the hypothesis that incompatible physical object states correspond to incompatible brain states, and that the cognitive system must therefore resolve conflict among incompatible representations. In other words, comprehension of an object state-change comes at a competitive cost. We tested this hypothesis by measuring univariate amplitude-modulation and multivariate pattern-similarity of the fMRI BOLD response within specific brain areas while subjects performed state-change comprehension tasks. These measured brain areas were functionally and anatomically defined as either specifically sensitive to semantic conflict (left pVLPFC) or to underlie the visual representation of objects and their features (early and late VVC).

In Chapter 2, we described a pair of fMRI experiments that test whether comprehension of object state-change described through language evokes a neural response in prefrontal cortex that is the same as for known forms of conflict. Specific manipulations of object state-change in these two experiments complement one another. In the first experiment, the same object was described as being changed either substantially or minimally by one of two actions. In the second experiment, the same action was described as either substantially or minimally changing one of two objects. By separately varying the described action and the described object across experiments, we avoid differences in pVLPFC activation being due to changes in the verb alone or the object alone. On a subject-specific basis, we identified voxels most responsive to conflict in a Stroop color-word interference task, and discovered a triple dissociation across ROIs in left pVLPFC, left MFG, and left MTG. Voxels in left pVLPFC most responsive to Stroop conflict were also responsive to the object state-change manipulation, yet were not responsive to the imageability of described events; voxels in left MFG responsive to Stroop conflict were not responsive even to language; and voxels in left MTG that were responsive to language and imageability were not responsive to object-change. Results from the experiments in Chapter 2 suggest that, when representing object state-change, incompatible representations of an object compete in working memory, and the greater the difference between the initial and end states of an object, the greater the conflict.

In Chapter 3, we went beyond inferring the maintenance of multiple incompatible object state representations based on the need for control from frontal cortex. At the same time that we measured the prefrontal conflict response, we used multi-voxel pattern analysis to directly measure distributed object representations in ventral visual cortex when an initially depicted object was imagined to be minimally or substantially changed by a described action. We found that the similarity of object states before and after a described event predicts not only the strength of the prefrontal cortex conflict response, but also the multivariate pattern-similarity of brain states in early visual cortex. In early visual cortex, multivariate pattern-similarity across time points before and after a described action was reliably reduced when the object was substantially changed, compared to when the object was minimally changed. In late visual cortex, multivariate pattern-similarity across time points was invariant to object state-change. Moreover, multivariate pattern-similarity in early visual cortex predicts the strength of prefrontal cortex conflict response even better than do the stimulus ratings of object state-change. Results suggest that distinct states of an object correspond to distinct visual cortex representations, and that the greater the dissimilarity between object states, the greater the dissimilarity between brain states, and the greater the conflict.

Considered together, the three fMRI experiments reported here suggest that distinct and incompatible representations of an object compete when representing object state-change. Below, we first address specific questions regarding the nature of competing object representations and the mechanisms involved in resolving this conflict. We then relate our present findings to object-based research in the field of visual attention, which we find to synergistically inform and be informed by our understanding of object state-change and semantic conflict.

Simulation versus Interference

Because the left pVLPFC Stroop-conflict ROI in each of the three experiments was functionally and anatomically constrained to include only voxels most responsive to semantic conflict, we interpret the observed effect of object state-change on signal amplitude in this ROI as reflecting conflict between incompatible object states. However, a statistical relationship between any independent variable and the signal amplitude of an ROI does not by itself allow a strong inference about the presence of a particular cognitive process (Friston & Price, 2003; Henson, 2005; Poldrack, 2006). Indeed, an alternative account of the observed parametric effects is that signal amplitude in left pVLPFC is driven by mental simulation of object state-change, as opposed to conflict between object-state representations (cf. Barsalou, 1999; Barsalou, Simmons, Barbey, & Wilson, 2003). According to the proposed conflict account of signal amplitude in left pVLPFC, state-change comprehension requires the cognitive system to maintain multiple incompatible representations of an object (changed and unchanged), and signal amplitude in left pVLPFC depends on the amount conflict between these incompatible object representations. According to a *simulation account* of left pVLPFC signal amplitude, the cognitive system would maintain only a single representation of acorn, and serially transform this representation as needed. The more an object is changed in state during an event, the more information must be inferred to derive the context-appropriate representation of the same object in its new state. In this case, signal change in left pVLPFC would depend on the amount of simulation required to comprehend the event sequence. We can, however, rule out a simulation account of the data by considering (1) the temporal-sequence manipulation in Experiment 1 of Chapter 2, and (2) the univariate amplitude-modulation effect described in Chapter 3 for left pVLPFC.

The temporal-sequence manipulation in Experiment 1 of Chapter 2 particularly is useful for distinguishing between a conflict account and a simulation account of the object state-change effects in left pVLPFC. In that experiment, multiple distinct representations of an object were introduced in the first sentence of substantial state-change items. For instance, an intact acorn and a cracked acorn are each implied by the first sentence “The squirrel will crack the acorn.” In the second sentence of these items, a temporal connective ('and then' or 'but first'), determined whether the object-state in focus is the changed state of the object or its original state. For instance, the temporal connective determines whether the acorn in focus is cracked or intact in the sentence "And then / But first the squirrel will lick the acorn." Conflict and simulation accounts make different predictions regarding the temporal context manipulation in Experiment 1. The conflict account predicts that there will always be greater pVLPFC activation when an object is changed in state, regardless of the temporal sequence. The simulation account predicts an interaction with temporal context in Experiment 1, because in the 'and then' case, the state computed at the end of the first sentence is identical to that referred to at the end of the second (but would be different in the 'but first' case). Insofar as the data from Experiment 1 revealed a main effect for state-change and no interaction with temporal sequence, a conflict account fits the data better than a simulation account, suggesting that the single-instantiation account is unlikely.

Data from Chapter 3 are also useful in distinguishing between conflict and simulation accounts of left pVLPFC activation. The design of the experiment in Chapter 3 permitted us to separately model each trial component: the object before state-change, the object during state-change, and the object after state-change. A simulation account predicts that, though substantial state-changes will correspond to increased pVLPFC signal amplitude *during* the state-change, there should be no difference between minimal and substantial state-change conditions in the pVLPFC amplitude-modulation measure (i.e., no difference in signal amplitude between the pre-action and post-action trial components). However, as predicted by the proposed conflict account, we found that the extent of pVLPFC amplitude-modulation was predicted by both the rated state-change of the item and the corresponding pattern-similarity in visual cortex. Thus, both the temporal-sequence data in Chapter 2 and the amplitude-modulation data in Chapter 3 strengthen the inference made here that condition-wise and item-wise differences in left pVLPFC signal amplitude are driven by conflict between incompatible representations of an object.

Typicality of Object States

Typicality may affect the saliency of the object-state representations. In many of the experimental items in Chapter 2, the described object begins in a very typical or canonical state (e.g., an intact acorn) and is altered to a more unusual state (e.g., a cracked acorn). Literature on typicality effects in language comprehension suggest that the strength of the initially activated object representation may partially determine the extent to which this initial representation remains active even after the contextually appropriate object representation has been computed (e.g., Rosch, 1978; Nosofsky, 1988; Southgate & Meints, 2000). Also, in computational models of lexical ambiguity in the comprehension of polysemous words, mental representations of word meanings are viewed as stable states within a semantic space that is shaped not only by context, but also by the relative frequency of word interpretations (Gernsbacher & St John, 2001; Klein & Murphy, 2001; Rodd, Gaskell, & Marslen-Wilson, 2004). Thus, though both the cracked and intact acorn representations are available to the cognitive system in the example above, the intact acorn representation may be more salient because it is closer to the prototypical acorn. Interestingly, these models of word typicality suggest that there should be less conflict for state-change for item such as “the musician will tune the piano," in which in the object goes from a less typical state (an out-of-tune piano) to a more typical state (a tuned piano).

While questions about the effects of object-state typicality on state-change comprehension promise an interesting avenue for future research, they are difficult to address within the data sets described in Chapters 2 and 3. In Chapter 2, the initial object state is unconstrained for minimal state-change items in each experiment. For instance, in the event "the squirrel will crack the acorn," it is implied that the initial state of the acorn is intact. However, in the event "the squirrel will sniff the acorn," it is not necessary or even implied that the initial state of the acorn is intact; the squirrel could just as likely sniff a cracked acorn. Thus, though we can measure object-state typicality for substantial state-change items in the Chapter 2 experiments, we cannot (without strong assumptions) measure object-state typicality for the minimal state-change items. The Chapter 3 experiment does not have this indeterminacy problem, as subjects are shown a photograph of the initial object state before each trial. However, in that experiment, the strength of the initial visual representation would likely mask any typicality effects of object states. In order to systematically vary the relative typicality of the initial state and end state of both substantially and minimally changed objects, future experiments will include an adjective that specifies the original state of each object. This adjective will constrain the initial object state for minimal state-change items as well as substantial state-change items, without visual memory processes masking possible typicality effects. In such an experiment, we may find that the relative typicality of the initial and end states of the object interacts with state-change. Such a pattern of results may suggest a two-factor conflict model (cf. Botvinick et al., 2001; Botvinick, Cohen, & Carter, 2004) for left pVLPFC, in which conflict and pVLPFC amplitude depend on the combined influence of the relative strength of incompatible object-state representations, and the similarity of the incompatible object-state representations to one another.

Object Rivalry

Similarity-based interference between distinct items in memory is not a new concept. Effects of semantic, syntactic, and phonological overlap among items has been observed in short-term memory (Baddeley & Dale, 1966; Shulman, 1971), long-term memory (Postman & Underwood, 1973; Anderson, Green, & McCulloch, 2000), and sentence comprehension (Gordon, Hendrick, Johnson, & Lee, 2006; Van Dyke & McElree, 2006). In each of these instances, greater similarity among items (i.e., semantic, syntactic, or phonological overlap) leads to greater interference. But this is precisely opposite to the interference effects that we observed in each fMRI experiment described in Chapters 2 and 3. In all three experiments, the amount of change that the object underwent *positively* correlated with the amplitude of the BOLD response in those Stroop-responsive voxels. That is, the more *dissimilar* alternative object representations were to one another, the greater the semantic conflict. Thus, it was not similarity-based interference that we found, but dissimilarity-based interference. This may be because greater change in object state corresponds to a greater the number of semantic features in conflict between object instantiations. We conjecture that this difference between distinct objects (similarity-based interference) and distinct instantiations of a single object (dissimilarity-based interference) has its roots in the fact that the distinct instantiations of an object across event-time (i.e., before and after state-change) are mutually exclusive –

they cannot co-exist. This mutual exclusivity must manifest in inhibition stemming from the non-overlapping elements of the instantiations (and hence the greater the difference between the two, the greater the mutual inhibition). Distinct objects, on the other hand, can co-exist no matter how similar; the greater the overlap between the objects' representations, the greater the interference, but differences between the objects do not have consequences for coexistence and are not inhibitory. This may be analogous to a percept that alternates between incompatible retinal inputs during binocular rivalry (Logothetis, Leopold, & Sheinberg, 1996; Tong, Nakayama, Vaughan, & Kanwisher, 1998), or a percept that alternates between mutually exclusive interpretations of an ambiguous figure during multistable perception (Sterzer, Kleinschmidt, & Rees, 2009; Long & Toppino, 2004).

An interesting avenue for future research will be to examine the difference between representing distinct objects versus representing distinct states of the same object. For instance, using a paradigm similar to that described in Chapter 3, a subject may see a photograph of a blue balloon, then follow task instructions to "remember the blue balloon" and then "inflate the blue balloon" and finally "look at the red balloon." In this case, the "before" and "after" object representations would be distinct objects that are visually similar and within the same category. If late visual cortex (which responds more strongly to intact objects than to feature-scrambled objects) codes for object *identity* (e.g., DiCarlo & Cox, 2007; Cichy, Chen, & Haynes, 2011) patterns of neural activation in this ROI may appear more dynamic than in the experiment described in Chapter 3. However, if late visual cortex codes for object *category* (e.g, Haxby et al., 2001; Kourtzi & Connor, 2011), multivariate pattern-similarity in this area may be invariant to this identity manipulation, just as it was to the state-change manipulation. To additionally manipulate object category within the same experimental paradigm, visual imagery instructions may proceed as “remember the balloon,” followed by “inflate the balloon,” followed by “look at the basketball.” In addition to VVC multivariate pattern-similarity, such manipulations of object identity and object category may also affect the observed functional connectivity relationship (i.e., VVC-predicted univariate amplitude-modulation) between early visual cortex and left pVLPFC.

Bridging Constructs: Object Files & Biased Competition

In the same way that functional connectivity can relate multivariate pattern-similarity in visual cortex to signal amplitude in prefrontal cortex, considerations of object state-change link models of object representation (e.g., Kahneman, Treisman, & Gibbs, 1992; Scholl, Pylyshyn, & Feldman, 2001) with models of the top-down control of attention (e.g., Desimone & Duncan, 1995; Desimone, 1998). Although these frameworks have been considered primarily in the context of visual perception, increasing evidence points to the cognitive and neural overlap of the cognitive and neural systems that guide “external attention” to perceptual representations, and “internal attention” to mental representations (Nobre et al., 2004; Chun et al., 2011).

The “object files” construct in visual attention is particularly useful for considering the cognitive mechanisms that might link object states to one another. In this construct, object files are mid-level representations for identifying and tracking objects through time and space (Kahneman et al., 1992; Xu & Chun, 2009). When a visual stimulus is attended, the observer must determine whether this stimulus is novel or belongs to an existing object file. If the stimulus is novel, a new object file is established, and is maintained even after the stimulus is out of sight (e.g., behind an occluder). If a stimulus includes features that match those of an existing object file, the observer automatically retrieves that object's past characteristics, which in turn influence the perceptual experience of the stimulus. Importantly, though the visual system typically prioritizes spatiotemporal information in assigning object files (e.g., two different-looking objects are treated as the same when one transitions smoothly to the other, while two similar-looking objects are treated as different when they appear over time discontinuously), semantic knowledge can influence and override spatiotemporal information. Whether the visual system tolerates interruptions of spatiotemporal continuity depends both on general knowledge, such as naïve physics, and specific semantic and episodic memories for the action affordances and potential states of each object (Carey & Xu, 2001). Two object instantiations (e.g., an egg that is broken, or a frog that turns into a prince) can be perceived as the same object despite discontinuities, if the initial object state and an intervening action together suggest a state-change.

Biased competition refers to the process through which top-down signals guide competitive interactions between mutually inhibitory ensembles of interconnected neurons (Desimone & Duncan, 1995; Kastner & Ungerleider, 2001). In this model, the prefrontal cortex influences attention through excitatory pathways that increase the firing rate within neural populations of low-level visual cortex that code for specific task-relevant features. In turn, increased firing rate of these feature-specific neural populations inhibits the firing rate of other surrounding neural populations. Kan & Thompson-Schill (2004) extended the biased competition model beyond perception, to semantic retrieval.

Attention to competing internal representations (e.g., incompatible object states) is described a two-component process of lateral inhibition and top-down constraint.

Data reported here suggest that competition between object states is a necessary component of event cognition, and that the visual attention frameworks of object files and biased competition are together useful in modeling state-change comprehension. Through the lens of object files, we can better understand how the cognitive system can treat two completely dissimilar neural representations as a single object. And through the lens of biased competition, we can better understand how alternative states of the same object compete in ventral visual cortex, at the same that task-specific neural patterns in prefrontal cortex bias these feature-based neural patterns toward the context-appropriate representation of an object.

Conclusions

Event comprehension often requires us to represent states of the world that are necessarily mutually exclusive from one another. Through a series of functional magnetic resonance imaging experiments, we test the hypothesis that, when an object is described as changing state during an event, the cognitive system must resolve conflict between the resulting incompatible brain states. In Chapter 2, we show that the degree of object state-change entailed by a described event predicts fMRI signal amplitude in left pVLPFC, an area known to be sensitive to semantic conflict, and that this neural response specifically overlaps with conflict-dependent signal on a Stroop interference task. By separately varying the described action and the described object across Experiments 1 and 2, we avoid changes in left pVLPFC activation being due to changes in the verb alone (Expt. 1) or the object alone (Expt. 2). In Chapter 3, we show that degree of object state-change also predicts the similarity of distributed patterns of fMRI activation in ventral visual cortex, and that this multivariate pattern-similarity of incompatible brain states in visual cortex is an even stronger predictor of pVLPFC activation than the rated degree of object state-change. Specific recruitment of pVLPFC during state-change comprehension suggests conflict at the level of semantic representations. Results from these experiments suggest that distinct and incompatible representations of an object compete when representing object state-change, that alternative states of an object correspond to distinct visual cortex representations, and that conflict measured in prefrontal cortex is mediated by the similarity of distributed representations in visual cortex.

REFERENCES

Allport, D. A., Styles, E. A., & Hsieh, S. (1994). Shifting intentional set: Exploring the dynamic control of tasks. In C. Umiltà & M. Moscovitchs (Eds.), *Attention and Performance 15: Conscious and Nonconscious Information Processing*. Cambridge, MA: The MIT Press.

Altmann, G. T., & Kamide, Y. (2009). Discourse-mediation of the mapping between language and the visual world: Eye movements and mental representation. *Cognition*, *111*(1), 55–71.

Amunts, K., Schleicher, A., Bürgel, U., Mohlberg, H., Uylings, H. B., & Zilles, K. (1999). Broca's region revisited: cytoarchitecture and intersubject variability. *The Journal of Comparative Neurology*, *412*(2), 319–341.

Anderson, M. C., Green, C., & McCulloch, K. C. (2000). Similarity and inhibition in long-term memory: Evidence for a two-factor theory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *26*(5), 1141.

Baddeley, A. D., & Dale, H. C. A. (1966). The effect of semantic similarity on retroactive interference in long-and short-term memory. *Journal of Verbal Learning and Verbal Behavior*, *5*(5), 417–420.

Badre, D., & Wagner, A. D. (2007). Left ventrolateral prefrontal cortex and the cognitive control of memory. *Neuropsychologia*, *45*(13), 2883–2901.

Barsalou, L. W. (1999). Perceptions of perceptual symbols. *Behavioral and Brain Sciences*, *22*(04), 637–660.

Barsalou, L. W., Kyle Simmons, W., Barbey, A. K., & Wilson, C. D. (2003). Grounding conceptual knowledge in modality-specific systems. *Trends in Cognitive Sciences*, *7*(2), 84–91.

Beauvois, M. F., & Derouesne, J. (1981). Lexical or orthographic agraphia. In J. Davidoff (Ed.), *Brain and Behavior: Critical Concepts in Psychology*. New York, NY: Routledge.

Bedny, M., McGill, M., & Thompson-Schill, S. L. (2008). Semantic adaptation and competition during word comprehension. *Cerebral Cortex*, *18*(11): 2574-2585.

Bedny, Marina, Aguirre, G. K., & Thompson-Schill, S. L. (2007). Item analysis in functional magnetic resonance imaging. *Neuroimage*, *35*(3), 1093–1102.

Binder, J. R., Desai, R. H., Graves, W. W., & Conant, L. L. (2009). Where Is the Semantic System? A Critical Review and Meta-Analysis of 120 Functional Neuroimaging Studies. *Cerebral Cortex*, *19*(12), 2767 –2796.

Blumstein, S. E., Cooper, W. E., Zurif, E. B., & Caramazza, A. (1977). The perception and production of voice-onset time in aphasia. *Neuropsychologia*, *15*(3), 371–372.

Blumstein, S. E., Myers, E. B., & Rissman, J. (2005). The perception of voice onset time: An fMRI investigation of phonetic category structure. *Journal of Cognitive Neuroscience*, *17*(9), 1353–1366.

Botvinick, M. M., Braver, T. S., Barch, D. M., Carter, C. S., & Cohen, J. D. (2001). Conflict monitoring and cognitive control. *Psychological Review*, *108*(3), 624.

Botvinick, M. M., Cohen, J. D., & Carter, C. S. (2004). Conflict monitoring and anterior cingulate cortex: an update. *Trends in Cognitive Sciences*, *8*(12), 539–546.

Bower, G. H. (2000). A brief history of memory research. *The Oxford Handbook of Memory*, 3–32.

Brysbaert, M., & New, B. (2009). Moving beyond Kučera and Francis: A critical evaluation of current word frequency norms and the introduction of a new and improved word frequency measure for American English. *Behavior Research Methods*, *41*(4), 977–990.

Burke, R. J. (2009). *Roger's Reference: The Complete Homonym/Homophone Dictionary (7th edition)*. Educational Multimedia Publishing.

Carey, S., & Xu, F. (2001). Infants' knowledge of objects: Beyond object files and object tracking. *Cognition*, *80*(1-2), 179–213.

Carrasco, M. (2011). Visual attention. *Vision Research*, *51*, 1484-1525.

Carter, C. S., Mintun, M., & Cohen, J. D. (1995). Interference and facilitation effects during selective attention: An H215O PET study of Stroop task performance. *Neuroimage*, *2*(4), 264–272.

Chambers, C. D., Payne, J. M., Stokes, M. G., & Mattingley, J. B. (2004). Fast and slow parietal pathways mediate spatial attention. *Nature Neuroscience*, *7*(3), 217–218.

Chaminade, T., Meltzoff, A. N., & Decety, J. (2005). An fMRI study of imitation: action representation and body schema. *Neuropsychologia*, *43*(1), 115–127.

Chun, M. M., Golomb, J. D., & Turk-Browne, N. B. (2011). A taxonomy of external and internal attention. *Annual Review of Psychology*, *62*, 73–101.

Cichy, R. M., Chen, Y., & Haynes, J. D. (2011). Encoding the identity and location of objects in human LOC. *Neuroimage*, *54*(3), 2297–2307.

Cohen, J. D., & Huston, T. A. (1994). Progress in the use of interactive models for understanding attention and performance. In C. Umiltà & M. Moscovitchs (Eds.), *Attention and Performance 15: Conscious and Nonconscious Information Processing*. Cambridge, MA: The MIT Press.

Coltheart, M., Davelaar, E., Jonasson, T., & Besner, D. (1977). Access to the internal lexicon. In S. Dornic (Ed.), *Attention and Performance VI*. Hillsdale, NJ: Erlbaum.

Cooper, R. M. (1974). The control of eye fixation by the meaning of spoken language: A new methodology for the real-time investigation of speech perception, memory, and language processing. *Cognitive Psychology*, *6*(1), 84-107

Cox, R. W. (1996). AFNI: software for analysis and visualization of functional magnetic resonance neuroimages. *Computers and Biomedical Research*, *29*(3), 162–173.

D'Esposito, M., Postle, B. R., Jonides, J., & Smith, E. E. (1999). The neural substrate and temporal dynamics of interference effects in working memory as revealed by event-related functional MRI. *Proceedings of the National Academy of Sciences*, *96*(13), 7514.

Derrfuss, J., Brass, M., Neumann, J., & Von Cramon, D. Y. (2005). Involvement of the inferior frontal junction in cognitive control: Meta-analyses of switching and Stroop studies. *Human brain mapping*, *25*(1), 22–34.

Desimone, R. (1998). Visual attention mediated by biased competition in extrastriate visual cortex. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *353*(1373), 1245–1255.

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, *18*(1), 193–222.

DiCarlo, J. J., & Cox, D. D. (2007). Untangling invariant object recognition. *Trends in cognitive sciences*, *11*(8), 333–341.

Duffy, S. A., Morris, R. K., & Rayner, K. (1988). Lexical Ambiguity and Fixation Times in Reading. *Journal of Memory and Language*, *27*(4), 429–446.

Eickhoff, S. B., Stephan, K. E., Mohlberg, H., Grefkes, C., Fink, G. R., Amunts, K., & Zilles, K. (2005). A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. *Neuroimage*, *25*(4), 1325–1335.

Farmer, T. A., Cargill, S. A., Hindy, N. C., Dale, R., & Spivey, M. J. (2007). Tracking the Continuity of Language Comprehension: Computer Mouse Trajectories Suggest Parallel Syntactic Processing. *Cognitive Science*, *31*(5), 21.

Fedorenko, E., & Kanwisher, N. (2009). Neuroimaging of language: Why hasn't a clearer picture emerged? *Language and Linguistics Compass*, *3*(4), 839–865.

Feredoes, E., & Postle, B. R. (2010). Prefrontal Control of Familiarity and Recollection in Working Memory. *Journal of Cognitive Neuroscience*, *22*(2), 323–330.

Feredoes, E., Tononi, G., & Postle, B. R. (2006). Direct evidence for a prefrontal contribution to the control of proactive interference in verbal working memory. *Proceedings of the National Academy of Sciences*, *103*(51), 19530–19534.

Friston, K. J., & Price, C. J. (2003). Degeneracy and redundancy in cognitive anatomy. *Trends in Cognitive Sciences*, *7*(4), 151–152.

Fuster, J. M. (2008). *The Prefrontal Cortex*. Academic Press.

Gernsbacher, M. A., & St John, M. F. (2001). Modeling suppression in lexical access.

Gilbert, S. J., & Shallice, T. (2002). Task switching: A PDP model. *Cognitive psychology*, *44*(3), 297–337.

Glover, S. (2004). Separate visual representations in the planning and control of action. *Behavioral and Brain Sciences*, *27*(01), 3–24.

Gordon, P. C., Hendrick, R., Johnson, M., & Lee, Y. (2006). Similarity-based interference during language comprehension: Evidence from eye tracking during reading. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *32*(6), 1304.

Grill-Spector, K., & Malach, R. (2004). The human visual cortex. *Annu. Rev. Neurosci.*, *27*, 649–677.

Haxby, J. V., Gobbini, M. I., Furey, M. L., Ishai, A., Schouten, J. L., & Pietrini, P. (2001). Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science*, *293*(5539), 2425.

Hein, G., & Knight, R. T. (2008). Superior Temporal Sulcus-It's My Area: Or Is It? *Journal of Cognitive Neuroscience*, *20*(12), 2125–2136.

Henson, R. (2005). What can functional neuroimaging tell the experimental psychologist? *The Quarterly Journal of Experimental Psychology Section A*, *58*(2), 193–233.

Hermsdörfer, J., Goldenberg, G., Wachsmuth, C., Conrad, B., Ceballos-Baumann, A., Bartenstein, P., Schwaiger, M., et al. (2001). Cortical correlates of gesture processing: clues to the cerebral mechanisms underlying apraxia during the imitation of meaningless gestures. *Neuroimage*, *14*(1), 149–161.

Hindy, N. C., Altmann, G. T. M., Kalenik, E., & Thompson-Schill, S. L. (2012). The Effect of Object State-Changes on Event Processing: Do Objects Compete with Themselves? *The Journal of Neuroscience*, *32*(17), 5795–5803.

Hindy, N. C., Hamilton, R., Houghtling, A. S., Coslett, H., & Thompson-Schill, S. L. (2009). Computer-mouse tracking reveals TMS disruptions of prefrontal function during semantic retrieval. *Journal of Neurophysiology*, *102*(6), 3405.

January, D., Trueswell, J. C., & Thompson-Schill, S. L. (2009). Co-localization of Stroop and Syntactic Ambiguity Resolution in Broca's Area: Implications for the Neural Basis of Sentence Processing. *Journal of Cognitive Neuroscience*, *21*(12), 2434–2444.

Johnson, M. K. (1992). MEM: Mechanisms of recollection. *Journal of Cognitive Neuroscience*, *4*(3), 268–280.

Johnson, M. R., Mitchell, K. J., Raye, C. L., D'Esposito, M., & Johnson, M. K. (2007). A brief thought can modulate activity in extrastriate visual areas: Top-down effects of refreshing just-seen visual stimuli. *Neuroimage*, *37*(1), 290–299.

Jonides, J., Lewis, R. L., Nee, D. E., Lustig, C. A., Berman, M. G., & Moore, K. S. (2008). The mind and brain of short-term memory. *Annu. Rev. Psychol.*, *59*, 193–224.

Jonides, J., & Nee, D. E. (2006). Brain mechanisms of proactive interference in working memory. *Neuroscience*, *139*(1), 181–193.

Jonides, J., Smith, E. E., Marshuetz, C., Koeppe, R. A., & Reuter-Lorenz, P. A. (1998). Inhibition in verbal working memory revealed by brain activation. *Proceedings of the National Academy of Sciences*, *95*(14), 8410.

Kahneman, D., Treisman, A., & Gibbs, B. J. (1992). The reviewing of object files: Object-specific integration of information. *Cognitive Psychology*, *24*(2), 175–219.

Kan, I. P., & Thompson-Schill, S. L. (2004). Selection from perceptual and conceptual representations. *Cognitive, Affective, & Behavioral Neuroscience*, *4*(4), 466–482.

Kintsch, W. (1988). The role of knowledge in discourse comprehension: a construction-integration model. *Psychological Review*, *95*(2), 163.

Klein, D. E., & Murphy, G. L. (2002). Paper has been my ruin: conceptual relations of polysemous senses. *Journal of Memory and Language*, *47*(4), 548–570.

Kourtzi, Z., & Kanwisher, N. (2001). Representation of perceived object shape by the human lateral occipital complex. *Science*, *293*(5534), 1506–1509.

Kourtzi, Zoe, & Connor, C. E. (2011). Neural Representations for Object Perception: Structure, Category, and Adaptive Coding. *Annual Review of Neuroscience*, *34*(1), 45–67.

Kriegeskorte, N., Goebel, R., & Bandettini, P. (2006). Information-based functional brain mapping. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(10), 3863–3868.

Kriegeskorte, N., Mur, M., & Bandettini, P. (2008). Representational similarity analysis–connecting the branches of systems neuroscience. *Frontiers in Systems Neuroscience*, *2*, 4.

Kuhl, B. A., Rissman, J., Chun, M. M., & Wagner, A. D. (2011). Fidelity of neural reactivation reveals competition between memories. *Proceedings of the National Academy of Sciences*, *108*(14), 5903-5908.

Liu, X., Banich, M. T., Jacobson, B. L., & Tanabe, J. L. (2006). Functional dissociation of attentional selection within PFC: response and non-response related aspects of attentional selection as ascertained by fMRI. *Cerebral Cortex*, *16*(6), 827.

Logothetis, N. K., Leopold, D. A., & Sheinberg, D. L. (1996). What is rivalling during binocular rivalry? *Nature*, *380*, 621–624.

Long, G. M., & Toppino, T. C. (2004). Enduring interest in perceptual ambiguity: Alternating views of reversible figures. *Psychological Bulletin*, *130*(5), 748–768.

MacLeod, C. M. (1991). Half a century of research on the Stroop effect: An integrative review. *Psychological Bulletin*, *109*(2), 163–203.

MacLeod, C. M. (2005). The Stroop task in cognitive research. In A. Wenzel & D. C. Rubin (Eds.), *Cognitive Methods and Their Application to Clinical Research* (pp. 41-62). Washington, DC: American Psychological Association.

MacLeod, C. M., & MacDonald, P. A. (2000). Interdimensional interference in the Stroop effect: Uncovering the cognitive and neural anatomy of attention. *Trends in Cognitive Sciences*, *4*(10), 383–391.

Marr, D. (1982). *Vision: A Computational Investigation into the Human Representation and Processing of Visual Information*. New York, NY: Henry Holt and Co.

Marr, D., & Poggio, T. (1979). A computational theory of human stereo vision. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, *204*(1156), 301–328.

Martin, A. (2007). The representation of object concepts in the brain. *Annual Review of Psychology*, *58*, 25–45.

Metzler, C. (2001). Effects of left frontal lesions on the selection of context-appropriate meanings. *Neuropsychology*, *15*(3), 315–328.

Milham, M. P., Banich, M. T., Webb, A., Barad, V., Cohen, N. J., Wszalek, T., & Kramer, A. F. (2001). The relative involvement of anterior cingulate and prefrontal cortex in attentional control depends on nature of conflict. *Cognitive Brain Research*, *12*(3), 467–473.

Miller, E. K. (2000). The prefrontal cortex and cognitive control. *Nature Reviews. Neuroscience*, *1*(1), 59–65.

Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience*, *24*(1), 167–202.

Monsell, S. (1978). Recency, immediate recognition memory, and reaction time* 1. *Cognitive Psychology*, *10*(4), 465–501.

Mort, D. J., Malhotra, P., Mannan, S. K., Rorden, C., Pambakian, A., Kennard, C., & Husain, M. (2003). The anatomy of visual neglect. *Brain*, *126*(9), 1986–1997.

Nobre, A. C., Coull, J. T., Maquet, P., Frith, C. D., Vandenberghe, R., & Mesulam, M. M. (2004). Orienting attention to locations in perceptual versus mental representations. *Journal of Cognitive Neuroscience*, *16*(3), 363–373.

Norman, K. A., Polyn, S. M., Detre, G. J., & Haxby, J. V. (2006). Beyond mind-reading: multi-voxel pattern analysis of fMRI data. *Trends in Cognitive Sciences*, *10*(9), 424–430.

Nosofsky, R. M. (1988). Exemplar-based accounts of relations between classification, recognition, and typicality. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *14*(4), 700.

Novick, J. M., Trueswell, J. C., & Thompson-Schill, S. L. (2005). Cognitive control and parsing: Reexamining the role of Broca's area in sentence comprehension. *Cognitive, Affective, & Behavioral Neuroscience*, *5*(3), 263.

O'Reilly, R. C., Herd, S. A., & Pauli, W. M. (2010). Computational models of cognitive control. *Current Opinion in Neurobiology*, *20*(2), 257–261.

Pardo, J. V., Pardo, P. J., Janer, K. W., & Raichle, M. E. (1990). The anterior cingulate cortex mediates processing selection in the Stroop attentional conflict paradigm. *Proceedings of the National Academy of Sciences*, *87*(1), 256.

Park, S., Chun, M. M., & Johnson, M. K. (2010). Refreshing and integrating visual scenes in scene-selective cortex. *Journal of Cognitive Neuroscience*, *22*(12), 2813–2822.

Poldrack, R. A. (2006). Can cognitive processes be inferred from neuroimaging data? *Trends in Cognitive Sciences*, *10*(2), 59–63.

Postman, L., & Underwood, B. J. (1973). Critical issues in interference theory. *Memory & Cognition*, *1*(1), 19–40.

Pylyshyn, Z. (1989). The role of location indexes in spatial perception: A sketch of the FINST spatial-index model. *Cognition*, *32*(1), 65–97.

Robinson, G., Blair, J., & Cipolotti, L. (1998). Dynamic aphasia: an inability to select between competing verbal responses? *Brain*, *121*(1), 77.

Robinson, G., Shallice, T., & Cipolotti, L. (2005). A failure of high level verbal response selection in progressive dynamic aphasia. *Cognitive Neuropsychology*, *22*(6), 661–694.

Rodd, J. M., Gaskell, M. G., & Marslen-Wilson, W. D. (2004). Modelling the effects of semantic ambiguity in word recognition. *Cognitive Science*, *28*(1), 89–104.

Rosch, E. (1978). Principles of categorization. *Concepts: Core Readings*, 189–206.

Rougier, N. P., Noelle, D. C., Braver, T. S., Cohen, J. D., & O'Reilly, R. C. (2005). Prefrontal cortex and flexible cognitive control: Rules without symbols. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(20), 7338.

Saxe, R., Brett, M., & Kanwisher, N. (2006). Divide and conquer: a defense of functional localizers. *Neuroimage*, *30*(4), 1088–1096.

Scholl, B. J., Pylyshyn, Z. W., & Feldman, J. (2001). What is a visual object? Evidence from target merging in multiple object tracking. *Cognition*, *80*(1-2), 159–177.

Schrödinger, E. (1935). Die gegenwärtige Situation in der Quantenmechanik. *Naturwissenschaften*, *23*(49), 823–828.

Seidenberg, M. S., & McClelland, J. L. (1989). A distributed, developmental model of word recognition and naming. *Psychological Review*, *96*(4), 523.

Shulman, H. G. (1971). Similarity effects in short-term memory. *Psychological Bulletin*, *75*(6), 399.

Southgate, V., & Meints, K. (2000). Typicality, naming, and category membership in young children. *Cognitive Linguistics*, *11*, 5–16.

Sternberg, S. (1966). High-speed scanning in human memory. *Science*, *153*(736), 652–4.

Sterzer, P., Kleinschmidt, A., & Rees, G. (2009). The neural bases of multistable perception. *Trends in Cognitive Sciences*, *13*(7), 310–318.

Stroop, J. R. (1935). Studies of interference in serial verbal reactions. *Journal of Experimental Psychology*, *18*, 643–662.

Tanenhaus, M. K., Spivey-Knowlton, M. J., Eberhard, K. M., & Sedivy, J. C. (1995). Integration of visual and linguistic information in spoken language comprehension. *Science*, *268*(5217), 1632–1634.

Thompson-Schill, S. L, D'Esposito, M., Aguirre, G. K., & Farah, M. J. (1997). Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. *Proceedings of the National Academy of Sciences*, *94*(26), 14792–14797.

Thompson-Schill, S. L, Jonides, J., Marshuetz, C., Smith, E. E., D'Esposito, M., Kan, I. P., Knight, R. T., et al. (2002). Effects of frontal lobe damage on interference effects in working memory. *Cognitive, Affective, & Behavioral Neuroscience*, *2*(2), 109–120.

Thompson-Schill, S. L., Bedny, M., & Goldberg, R. F. (2005). The frontal lobes and the regulation of mental activity. *Current Opinion in Neurobiology*, *15*(2), 219–224.

Thompson-Schill, S. L., & Botvinick, M. M. (2006). Resolving conflict: A response to Martin and Cheng (2006). *Psychonomic Bulletin & Review*, *13*(3), 402–408.

Thompson-Schill, S. L., D'Esposito, M., Aguirre, G. K., & Farah, M. J. (1997). Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. *Proceedings of the National Academy Sciences*, *94*, 14792–14797.

Thompson-Schill, S. L., D'Esposito, M., & Kan, I. P. (1999). Effects of Repetition and Competition on Activity in Left Prefrontal Cortex during Word Generation. *Neuron*, *23*, 513–522.

Thompson-Schill, S. L., Swick, D., Farah, M. J., D'Esposito, M., Kan, I. P., & Knight, R. T. (1998). Verb generation in patients with focal frontal lesions: A neuropsychological test of neuroimaging findings. *Proceedings of the National Academy Sciences*, *95*, 15855–15860.

Thompson-Schill, Sharon L, Bedny, M., & Goldberg, R. F. (2005). The frontal lobes and the regulation of mental activity. *Current Opinion in Neurobiology*, *15*(2), 219–224.

Tong, F., Nakayama, K., Vaughan, J. T., & Kanwisher, N. (1998). Binocular rivalry and visual awareness in human extrastriate cortex. *Neuron*, *21*(4), 753–759.

Turken, A. U., Swick, D., & others. (1999). Response selection in the human anterior cingulate cortex. *Nature Neuroscience*, *2*, 920–924.

Ullman, S. (2000). *High-level vision: Object recognition and visual cognition*. Cambridge, MA: The MIT Press.

Van Dyke, J. A., & McElree, B. (2006). Retrieval interference in sentence comprehension. *Journal of Memory and Language*, *55*(2), 157–166.

van Veen, V., & Carter, C. S. (2005). Separating semantic conflict and response conflict in the Stroop task: A functional MRI study. *Neuroimage*, *27*(3), 497–504.

Wager, T. D., Jonides, J., & Reading, S. (2004). Neuroimaging studies of shifting attention: a meta-analysis. *Neuroimage*, *22*(4), 1679–1693.

Weber, M., Thompson-Schill, S. L., Osherson, D., Haxby, J., & Parsons, L. (2009). Predicting judged similarity of natural categories from their neural representations. *Neuropsychologia*, *47*(3), 859–868.

Whitney, C., Kirk, M., O'Sullivan, J., Lambon Ralph, M. A., & Jefferies, E. (2011). The neural organization of semantic control: TMS evidence for a distributed network in left inferior frontal and posterior middle temporal gyrus. *Cerebral Cortex*, *21*(5), 1066.

Xu, Y., & Chun, M. M. (2009). Selecting and perceiving multiple visual objects. *Trends in Cognitive Sciences*, *13*(4), 167–174.

Zwaan, R. A., & Radvansky, G. A. (1998). Situation models in language comprehension and memory. *Psychological Bulletin*, *123*, 162–185.

Zysset, S., Müller, K., Lohmann, G., & Von Cramon, D. Y. (2001). Color-word matching Stroop task: Separating interference and response conflict. *Neuroimage*, *13*(1), 29–36.

APPENDIX A

Experiment 1 event comprehension items (object fixed, action varied). Full stimulus set of 120 items. Each subject saw each item in only one of the four conditions. All items contain the same object in all conditions.

A and B = action minimally changes object
C and D = action substantially changes object

1.
A) The lumberjack will point at the tree branch. But first, he will reach for the tree branch.
B) The lumberjack will point at the tree branch. And then, he will reach for the tree branch.
C) The lumberjack will saw off the tree branch. But first, he will reach for the tree branch.
D) The lumberjack will saw off the tree branch. And then, he will reach for the tree branch.

2.
A) The girl will gaze through the window. But first, she will kneel beside the window.
B) The girl will gaze through the window. And then, she will kneel beside the window.
C) The girl will open up the window. But first, she will kneel beside the window.
D) The girl will open up the window. And then, she will kneel beside the window.

3.
A) The boy will yell at the jack-in-the-box. But first, he will frown at the jack-in-the-box.
B) The boy will yell at the jack-in-the-box. And then, he will frown at the jack-in-the-box.
C) The boy will pop open the jack-in-the-box. But first, he will frown at the jack-in-the-box.
D) The boy will pop open the jack-in-the-box. And then, he will frown at the jack-in-the-box.

4.
A) The woman will pick out the apple. But first, she will talk about the apple.
B) The woman will pick out the apple. And then, she will talk about the apple.
C) The woman will bite into the apple. But first, she will talk about the apple.
D) The woman will bite into the apple. And then, she will talk about the apple.

5.
A) The child will lick the Popsicle. But first, she will grin at the Popsicle.
B) The child will lick the Popsicle. And then, she will grin at the Popsicle.
C) The child will unwrap the Popsicle. But first, she will grin at the Popsicle.
D) The child will unwrap the Popsicle. And then, she will grin at the Popsicle.

6.
A) The expert will examine the Rubik’s Cube. But first, he will explain the Rubik’s Cube.
B) The expert will examine the Rubik’s Cube. And then, he will explain the Rubik’s Cube.
C) The expert will solve the Rubik’s Cube. But first, he will explain the Rubik’s Cube.
D) The expert will solve the Rubik’s Cube. And then, he will explain the Rubik’s Cube.

7.
A) The boy will inspect the broken zipper. But first, he will complain about the zipper.
B) The boy will inspect the broken zipper. And then, he will complain about the zipper.
C) The boy will fix the broken zipper. But first, he will complain about the zipper
D) The boy will fix the broken zipper. And then, he will complain about the zipper.

8.
A) The child will tap the ketchup bottle. But first, he will comment on the ketchup bottle.
B) The child will tap the ketchup bottle. And then, he will comment on the ketchup bottle.
C) The child will open the ketchup bottle. But first, he will comment on the ketchup bottle.
D) The child will open the ketchup bottle. And then, he will comment on the ketchup bottle.

9.
A) The fireman will grip the fire hose. But first, he will ask about the hose.
B) The fireman will grip the fire hose. And then, he will ask about the hose.
C) The fireman will unravel the fire hose. But first, he will ask about the hose.
D) The fireman will unravel the fire hose. And then, he will ask about the hose.

10.
A) The grouch will curse at the alarm clock. But first, he will hit the alarm clock.
B) The grouch will curse at the alarm clock. And then, he will hit the alarm clock.
C) The grouch will turn off the alarm clock. But first, he will hit the alarm clock.
D) The grouch will turn off the alarm clock. And then, he will hit the alarm clock.

11.
A) The teenager will bang on the trashcan. But first, he will walk around the trashcan.
B) The teenager will bang on the trashcan. And then, he will walk around the trashcan.
C) The teenager will tip over the trashcan. But first, he will walk around the trashcan.
D) The teenager will tip over the trashcan. And then, he will walk around the trashcan.

12.
A) The mother will select the egg. But first, she will talk about the egg.
B) The mother will select the egg. And then, she will talk about the egg.
C) The mother will crack the egg. But first, she will talk about the egg.
D) The mother will crack the egg. And then, she will talk about the egg.

13.
A) The groomer will pet the dog. But first, he will feed the dog.
B) The groomer will pet the dog. And then, he will feed the dog.
C) The groomer will shave the dog. But first he will feed the dog.
D) The groomer will shave the dog. And then, he will feed the dog.

14.
A) The artist will stare at the blank canvas. But first, he will ponder the canvas.
B) The artist will stare at the blank canvas. And then, he will ponder the canvas.
C) The artist will paint on the blank canvas. But first, he will ponder the canvas.
D) The artist will paint on the blank canvas. And then, he will ponder the canvas.

15.
A) The boy will shake the empty water gun. But first, he will giggle about the water gun.
B) The boy will shake the empty water gun. And then, he will giggle about the water gun.
C) The boy will fill the empty water gun. But first, he will giggle about the water gun.
D) The boy will fill the empty water gun. And then, he will giggle about the water gun.

16.
A) The plumber will examine the pipe. But first, he will frown at the pipe.
B) The plumber will examine the pipe. And then, he will frown at the pipe.
C) The plumber will bend the pipe. But first, he will frown at the pipe.
D) The plumber will bend the pipe. And then, he will frown at the pipe.

17.
A) The bride will accept the gift. But first, she will give thanks for the gift.
B) The bride will accept the gift. And then, she will give thanks for the gift.
C) The bride will unwrap the gift. But first, she will give thanks for the gift.
D) The bride will unwrap the gift. And then, she will give thanks for the gift.

18.
A) The bartender will select the tequila bottle. But first, he will talk about the tequila bottle.
B) The bartender will select the tequila bottle. And then, he will talk about the tequila bottle.
C) The bartender will empty the tequila bottle. But first, he will talk about the tequila bottle.
D) The bartender will empty the tequila bottle. And then, he will talk about the tequila bottle.

19.
A) The sailor will hold onto the sail. But first, he will scowl at the sail.
B) The sailor will hold onto the sail. And then, he will scowl at the sail.
C) The sailor will take down the sail. But first, he will scowl at the sail.
D) The sailor will take down the sail. And then, he will scowl at the sail.

20.
A) The office worker will type on the keyboard. But first, he will complain about the keyboard.
B) The office worker will type on the keyboard. And then, he will complain about the keyboard.
C) The office worker will plug in the keyboard. But first, he will complain about the keyboard.
D) The office worker will plug in the keyboard. And then, he will complain about the keyboard.

21.
A) The squirrel will sniff the acorn. But first, it will lick the acorn.
B) The squirrel will sniff the acorn. And then, it will lick the acorn.
C) The squirrel will crack the acorn. But first, it will lick the acorn.
D) The squirrel will crack the acorn. And then, it will lick the acorn.

22.
A) The carpenter will sift through the toolbox. But first, he will frown at the toolbox.
B) The carpenter will sift through the toolbox. And then, he will frown at the toolbox.
C) The carpenter will open up the toolbox. But first, he will frown at the toolbox.
D) The carpenter will open up the toolbox. And then, he will frown at the toolbox.

23.
A) The gorilla will inspect the banana. But first, he will grunt at the banana.
B) The gorilla will inspect the banana. And then, he will grunt at the banana.
C) The gorilla will peel the banana. But first, he will grunt at the banana.
D) The gorilla will peel the banana. And then, he will grunt at the banana.

24.
A) The construction worker will bang on the wall. But first, he will frown at the wall.
B) The construction worker will bang on the wall. And then, he will frown at the wall.
C) The construction worker will knock down the wall. But first, he will frown at the wall.
D) The construction worker will knock down the wall. And then, he will frown at the wall.

25.
A) The boy will rub the coin. But first, he will grin at the coin.
B) The boy will rub the coin. And then, he will grin at the coin.
C) The boy will spin the coin. But first, he will grin at the coin.
D) The boy will spin the coin. And then, he will grin at the coin.

26.
A) The boy will examine his shoes. But first, he will brag about his shoes.
B) The boy will examine his shoes. And then, he will brag about his shoes.
C) The boy will untie his shoes. But first, he will brag about his shoes.
D) The boy will untie his shoes. And then, he will brag about his shoes.

27.
A) The teacher will point at the blackboard. But first, she will read from the blackboard.
B) The teacher will point at the blackboard. And then, she will read from the blackboard.
C) The teacher will draw on the blackboard. But first, she will read from the blackboard.
D) The teacher will draw on the blackboard. And then, she will read from the blackboard.

28.
A) The girl will pose behind the shirt. But first, she will ask about the shirt.
B) The girl will pose behind the shirt. And then, she will ask about the shirt.
C) The girl will hang up the shirt. But first, she will ask about the shirt.
D) The girl will hang up the shirt. And then, she will ask about the shirt.

29.
A) The tour guide will inspect the umbrella. But first, she will clench the umbrella.
B) The tour guide will inspect the umbrella. And then, she will clench the umbrella.
C) The tour guide will open the umbrella. But first, she will clench the umbrella.
D) The tour guide will open the umbrella. And then, she will clench the umbrella.

30.
A) The gymnast will examine the jump rope. But first, she will complain about the jump rope.
B) The gymnast will examine the jump rope. And then, she will complain about the jump rope.
C) The gymnast will cut the jump rope. But first, she will complain about the jump rope.
D) The gymnast will cut the jump rope. And then, she will complain about the jump rope.

31.
A) The airline pilot will admire his hat. But first, he will chat about his hat.
B) The airline pilot will admire his hat. And then, he will chat about his hat.
C) The airline pilot will remove his hat. But first, he will chat about his hat.
D) The airline pilot will remove his hat. And then, he will chat about his hat.

32.
A) The zookeeper will count the animals. But first, he will chat about the animals.
B) The zookeeper will count the animals. And then, he will chat about the animals.
C) The zookeeper will release the animals. But first, he will chat about the animals.
D) The zookeeper will release the animals. And then, he will chat about the animals.

33.
A) The teacher will glare at the paper. But first, she will reread the paper.
B) The teacher will glare at the paper. And then, she will reread the paper.
C) The teacher will mark up the paper. But first, she will reread the paper.
D) The teacher will mark up the paper. And then, she will reread the paper.

34.

A) The babysitter will trip over the toy truck. But first, she will grumble about the truck.
B) The babysitter will trip over the toy truck. And then, she will grumble about the truck.
C) The babysitter will put away the toy truck. But first, she will grumble about the truck.
D) The babysitter will put away the toy truck. And then, she will grumble about the truck.

35.
A) The secretary will search the files. But first, she will gripe about the files.
B) The secretary will search the files. And then, she will gripe about the files.
C) The secretary will shred the files. But first, she will gripe about the files.
D) The secretary will shred the files. And then, she will gripe about the files.

36.
A) The dog will nudge his food bowl. But first, he will smell his food bowl.
B) The dog will nudge his food bowl. And then, he will smell his food bowl.
C) The dog will empty his food bowl. But first, he will smell his food bowl.
D) The dog will empty his food bowl. And then, he will smell his food bowl.

37.
A) The boxer will step toward his opponent. But first, he will taunt his opponent.
B) The boxer will step toward his opponent. And then, he will taunt his opponent.
C) The boxer will knock out his opponent. But first, he will taunt his opponent.
D) The boxer will knock out his opponent. And then, he will taunt his opponent.

38.
A) The little girl will kiss her teddy bear. But first, she will talk to her teddy bear.
B) The little girl will kiss her teddy bear. And then, she will talk to her teddy bear.
C) The little girl will dress her teddy bear. But first, she will talk to her teddy bear.
D) The little girl will dress her teddy bear. And then, she will talk to her teddy bear.

39.
A) The aunt will count up the leftover Halloween candy. But first, she will grimace at the candy.
B) The aunt will count up the leftover Halloween candy. And then, she will grimace at the candy.
C) The aunt will dump out the leftover Halloween candy. But first, she will grimace at the candy.
D) The aunt will dump out the leftover Halloween candy. And then, she will grimace at the candy.

40.
A) The teenager will interpret the Magic 8-Ball. But first, she will chat about the Magic 8-Ball.
B) The teenager will interpret the Magic 8-Ball. And then, she will chat about the Magic 8-Ball.
C) The teenager will shake the Magic 8-Ball. But first, she will chat about the Magic 8-Ball.

D) The teenager will shake the Magic 8-Ball. And then, she will chat about the Magic 8-Ball.

41.
A) The maid will sit upon the messy bed. But first, she will complain about the bed.
B) The maid will sit upon the messy bed. And then, she will complain about the bed.
C) The maid will make up the messy bed. But first, she will complain about the bed.
D) The maid will make up the messy bed. And then, she will complain about the bed.

42.
A) The beaver will circle around the tree. But first, he will push against the tree.
B) The beaver will circle around the tree. And then, he will push against the tree.
C) The beaver will chew through the tree. But first, he will push against the tree.
D) The beaver will chew through the tree. And then, he will push against the tree.

43.
A) The farmer will select the pumpkin. But first, he will chat about the pumpkin
B) The farmer will select the pumpkin. And then, he will chat about the pumpkin.
C) The farmer will carve the pumpkin. But first, he will chat about the pumpkin.
D) The farmer will carve the pumpkin. And then, he will chat about the pumpkin.

44.
A) The boy will smile at the candle. But first, he will reach for the candle.
B) The boy will smile at the candle. And then, he will reach for the candle.
C) The boy will blow out the candle. But first, he will reach for the candle.
D) The boy will blow out the candle. And then, he will reach for the candle.

45.
A) The clown will rub the balloon. But first, he will laugh at the balloon.
B) The clown will rub the balloon. And then, he will laugh at the balloon.
C) The clown will inflate the balloon. But first, he will laugh at the balloon.
D) The clown will inflate the balloon. And then, he will laugh at the balloon.

46.
A) The student will write with the pencil. But first, she will clench the pencil.
B) The student will write with the pencil. And then, she will clench the pencil.
C) The student will sharpen up the pencil. But first, she will clench the pencil.
D) The student will sharpen up the pencil. And then, she will clench the pencil.

47.
A) The child will hide behind the plant. But first, he will jump over the plant.
B) The child will hide behind the plant. And then, he will jump over the plant.
C) The child will knock down the plant. But first, he will jump over the plant.
D) The child will knock down the plant. And then, he will jump over the plant.

48.

A) The musician will play the piano. But first, he will rave about the piano.
B) The musician will play the piano. And then, he will rave about the piano.
C) The musician will tune the piano. But first, he will rave about the piano.
D) The musician will tune the piano. And then, he will rave about the piano.

49.
A) The alley cat will follow the mouse. But first, she will hiss at the mouse.
B) The alley cat will follow the mouse. And then, she will hiss at the mouse.
C) The alley cat will injure the mouse. But first, she will hiss at the mouse.
D) The alley cat will injure the mouse. And then, she will hiss at the mouse.

50.
A) The toddler will look over the puzzle. But first, he will marvel at the puzzle.
B) The toddler will look over the puzzle. And then, he will marvel at the puzzle.
C) The toddler will break apart the puzzle. But first, he will marvel at the puzzle.
D) The toddler will break apart the puzzle. And then, he will marvel at the puzzle.

51.
A) The passerby will watch the bird. But first, she will call to the bird.
B) The passerby will watch the bird. And then, she will call to the bird.
C) The passerby will frighten the bird. But first, she will call to the bird.
D) The passerby will frighten the bird. And then, she will call to the bird.

52.
A) The girl will lie beside the diary. But first, she will read the diary.
B) The girl will lie beside the diary. And then, she will read the diary.
C) The girl will write in the diary. But first, she will read the diary.
D) The girl will write in the diary. And then, she will read the diary.

53.
A) The housepainter will check the ladder. But first, he will walk around the ladder.
B) The housepainter will check the ladder. And then, he will walk around the ladder.
C) The housepainter will extend the ladder. But first, he will walk around the ladder.
D) The housepainter will extend the ladder. And then, he will walk around the ladder.

54.
A) The ventriloquist will address the dummy. But first, he will make fun of the dummy.
B) The ventriloquist will address the dummy. And then, he will make fun of the dummy.
C) The ventriloquist will seat the dummy. But first, he will make fun of the dummy.
D) The ventriloquist will seat the dummy. And then, he will make fun of the dummy.

55.
A) The employee will stand beside the mannequin. But first, she will laugh at the mannequin.
B) The employee will stand beside the mannequin. And then, she will laugh at the mannequin.

C) The employee will dress up the mannequin. But first, she will laugh at the mannequin.
D) The employee will dress up the mannequin. And then, she will laugh at the mannequin.

56.
A) The customer will pick out the sunglasses. But first, she will ask about the sunglasses.
B) The customer will pick out the sunglasses. And then, she will ask about the sunglasses.
C) The customer will fold up the sunglasses. But first, she will ask about the sunglasses.
D) The customer will fold up the sunglasses. And then, she will ask about the sunglasses.

57.
A) The traveler will lay on the sleeping bag. But first, he will complain about the sleeping bag.
B) The traveler will lay on the sleeping bag. And then, he will complain about the sleeping bag.
C) The traveler will roll up the sleeping bag. But first, he will complain about the sleeping bag.
D) The traveler will roll up the sleeping bag. And then, he will complain about the sleeping bag.

58.
A) The young woman will admire the jewelry box. But first, she will comment on the jewelry box.
B) The young woman will admire the jewelry box. And then, she will comment on the jewelry box.
C) The young woman will open the jewelry box. But first, she will comment on the jewelry box.
D) The young woman will open the jewelry box. And then, she will comment on the jewelry box.

59.
A) The chef will weigh the onion. But first, she will smell the onion.
B) The chef will weigh the onion. And then, she will smell the onion.
C) The chef will chop the onion. But first, she will smell the onion.
D) The chef will chop the onion. And then, she will smell the onion.

60.
A) The woman will inspect the cello. But first, she will kneel beside the cello.
B) The woman will inspect the cello. And then, she will kneel beside the cello.
C) The woman will restring the cello. But first, she will kneel beside the cello.
D) The woman will restring the cello. And then, she will kneel beside the cello.

61.
A) The bully will pick on the boy. But first, he will shout at the boy.
B) The bully will pick on the boy. And then, he will shout at the boy.
C) The bully will knock down the boy. But first, he will shout at the boy.

D) The bully will knock down the boy. And then, he will shout at the boy.

62.
A) The passenger will clutch the seatbelt. But first, she will tug on the seatbelt.
B) The passenger will clutch the seatbelt. And then, she will tug on the seatbelt.
C) The passenger will buckle the seatbelt. But first, she will tug on the seatbelt.
D) The passenger will buckle the seatbelt. And then, she will tug on the seatbelt.

63.
A) The grandmother will look toward the lamp. But first, she will ask about the lamp.
B) The grandmother will look toward the lamp. And then, she will ask about the lamp.
C) The grandmother will turn on the lamp. But first, she will ask about the lamp.
D) The grandmother will turn on the lamp. And then, she will ask about the lamp.

64.
A) The child will poke at the rubber band. But first, he will grin at the rubber band.
B) The child will poke at the rubber band. And then, he will grin at the rubber band.
C) The child will stretch out the rubber band. But first, he will grin at the rubber band.
D) The child will stretch out the rubber band. And then, he will grin at the rubber band.

65.
A) The butler will praise the rug. But first, he will step over the rug.
B) The butler will praise the rug. And then, he will step over the rug.
C) The butler will unroll the rug. But first, he will step over the rug.
D) The butler will unroll the rug. And then, he will step over the rug.

66.
A) The student will sniff the pizza. But first, he will blow on the pizza.
B) The student will sniff the pizza. And then, he will blow on the pizza.
C) The student will slice the pizza. But first, he will blow on the pizza.
D) The student will slice the pizza. And then, he will blow on the pizza.

67.
A) The escaped parrot will screech at the birdcage. But first, he will climb the birdcage.
B) The escaped parrot will screech at the birdcage. And then, he will climb the birdcage.
C) The escaped parrot will knock down the birdcage. But first, he will climb the birdcage.
D) The escaped parrot will knock down the birdcage. And then, he will climb the birdcage.

68.
A) The athlete will sit beside the fan. But first, he will comment on the fan.
B) The athlete will sit beside the fan. And then, he will comment on the fan.
C) The athlete will turn on the fan. But first, he will comment on the fan.
D) The athlete will turn on the fan. And then, he will comment on the fan.

69.

A) The woman will peer behind the shower curtain. But first, she will frown at the shower curtain.
B) The woman will peer behind the shower curtain. And then, she will frown at the shower curtain.
C) The woman will hang up the shower curtain. But first, she will frown at the shower curtain.
D) The woman will hang up the shower curtain. And then, she will frown at the shower curtain.

70.
A) The child will poke the gingerbread man. But first, she will laugh at the gingerbread man.
B) The child will poke the gingerbread man. And then, she will laugh at the gingerbread man.
C) The child will decorate the gingerbread man. But first, she will laugh at the gingerbread man.
D) The child will decorate the gingerbread man. And then, she will laugh at the gingerbread man.

71.
A) The boy will inspect the kite. But first, he will compliment the kite.
B) The boy will inspect the kite. And then, he will compliment the kite.
C) The boy will unfold the kite. But first, he will compliment the kite.
D) The boy will unfold the kite. And then, he will compliment the kite.

72.
A) The musician will look over the saxophone. But first, she will ask about the saxophone.
B) The musician will look over the saxophone. And then, she will ask about the saxophone.
C) The musician will strap on the saxophone. But first, she will ask about the saxophone.
D) The musician will strap on the saxophone. And then, she will ask about the saxophone.

73.
A) The librarian will look at the book. But first, he will check out the book.
B) The librarian will look at the book. And then, he will check out the book.
C) The librarian will open up the book. But first, he will check out the book.
D) The librarian will open up the book. And then, he will check out the book.

74.
A) The ninja will grip the sword. But first, he will grin at the sword.
B) The ninja will grip the sword. And then, he will grin at the sword.
C) The ninja will unsheathe the sword. But first, he will grin at the sword.
D) The ninja will unsheathe the sword. And then, he will grin at the sword.

75.
A) The barista will point to the latte. But first, she will ring up the latte.
B) The barista will point to the latte. And then, she will ring up the latte.
C) The barista will top off the latte. But first, she will ring up the latte.
D) The barista will top off the latte. And then, she will ring up the latte.

76.
A) The artist will study the sculpture. But first, she will chat about the sculpture.
B) The artist will study the sculpture. And then, she will chat about the sculpture.
C) The artist will finish the sculpture. But first, she will chat about the sculpture.
D) The artist will finish the sculpture. And then, she will chat about the sculpture.

77.
A) The traffic cop will follow the speeding motorist. But first, he will recognize the motorist.
B) The traffic cop will follow the speeding motorist. And then, he will recognize the motorist.
C) The traffic cop will stop the speeding motorist. But first, he will recognize the motorist.
D) The traffic cop will stop the speeding motorist. And then, he will recognize the motorist.

78.
A) The flight attendant will locate the can of soda. But first, she will offer the can of soda.
B) The flight attendant will locate the can of soda. And then, she will offer the can of soda.
C) The flight attendant will open the can of soda. But first, she will offer the can of soda.
D) The flight attendant will open the can of soda. And then, she will offer the can of soda.

79.
A) The food critic will taste the coffee. But first, he will ask about the coffee.
B) The food critic will taste the coffee. And then, he will ask about the coffee.
C) The food critic will finish the coffee. But first, he will ask about the coffee.
D) The food critic will finish the coffee. And then, he will ask about the coffee.

80.
A) The carpenter will assess the floor. But first, he will step on the floor.
B) The carpenter will assess the floor. And then, he will step on the floor.
C) The carpenter will tile the floor. But first, he will step on the floor.
D) The carpenter will tile the floor. And then, he will step on the floor.

81.
A) The man will lean on the dishwasher. But first, he will comment on the dishwasher.
B) The man will lean on the dishwasher. And then, he will comment on the dishwasher.
C) The man will take apart the dishwasher. But first, he will comment on the dishwasher.

D) The man will take apart the dishwasher. And then, he will comment on the dishwasher.

82.
A) The hairdresser will caress the wig. But first, he will compliment the wig.
B) The hairdresser will caress the wig. And then, he will compliment the wig.
C) The hairdresser will braid the wig. But first, he will compliment the wig.
D) The hairdresser will braid the wig. And then, he will compliment the wig.

83.
A) The welder will clutch the blowtorch. But first, he will fiddle with the blowtorch.
B) The welder will clutch the blowtorch. And then, he will fiddle with the blowtorch.
C) The welder will light the blowtorch. But first, he will fiddle with the blowtorch.
D) The welder will light the blowtorch. And then, he will fiddle with the blowtorch.

84.
A) The girl will admire the flower. But first, she will sniff the flower.
B) The girl will admire the flower. And then, she will sniff the flower.
C) The girl will pluck the flower. But first, she will sniff the flower.
D) The girl will pluck the flower. And then, she will sniff the flower.

85.
A) The man will kick the gate. But first, he will lean on the gate.
B) The man will kick the gate. And then, he will lean on the gate.
C) The man will shut the gate. But first, he will lean on the gate.
D) The man will shut the gate. And then, he will lean on the gate.

86.
A) The paleontologist will dig around the fossil. But first, he will talk about the fossil.
B) The paleontologist will dig around the fossil. And then, he will talk about the fossil.
C) The paleontologist will dig up the fossil. But first, he will talk about the fossil.
D) The paleontologist will dig up the fossil. And then, he will talk about the fossil.

87.
A) The parking attendant will check the parking meter. But first, she will rest against the parking meter.
B) The parking attendant will check the parking meter. And then, she will rest against the parking meter.
C) The parking attendant will empty the parking meter. But first, she will rest against the parking meter.
D) The parking attendant will empty the parking meter. And then, she will rest against the parking meter.

88.
A) The owl will swoop toward the field mouse. But first, it will hoot at the field mouse.
B) The owl will swoop toward the field mouse. And then, it will hoot at the field mouse.
C) The owl will scare away the field mouse. But first, it will hoot at the field mouse.

D) The owl will scare away the field mouse. And then, it will hoot at the field mouse.

89.
A) The camper will look into the tent. But first, he will chat about the tent.
B) The camper will look into the tent. And then, he will chat about the tent.
C) The camper will put together the tent. But first, he will chat about the tent.
D) The camper will put together the tent. And then, he will chat about the tent.

90.
A) The exterminator will spot the cockroach. But first, he will talk about the cockroach.
B) The exterminator will spot the cockroach. And then, he will talk about the cockroach.
C) The exterminator will poison the cockroach. But first, he will talk about the cockroach.
D) The exterminator will poison the cockroach. And then, he will talk about the cockroach.

91.
A) The scuba diver will peer through the diving mask. But first, he will tug at the diving mask.
B) The scuba diver will peer through the diving mask. And then, he will tug at the diving mask.
C) The scuba diver will wipe clear the diving mask. But first, he will tug at the diving mask.
D) The scuba diver will wipe clear the diving mask. And then, he will tug at the diving mask.

92.
A) The dentist will prod the tooth. But first, he will talk about the tooth.
B) The dentist will prod the tooth. And then, he will talk about the tooth.
C) The dentist will remove the tooth. But first, he will talk about the tooth.
D) The dentist will remove the tooth. And then, he will talk about the tooth.

93.
A) The airline pilot will steer the airplane. But first, he will talk about the airplane.
B) The airline pilot will steer the airplane. And then, he will talk about the airplane.
C) The airline pilot will land the airplane. But first, he will talk about the airplane.
D) The airline pilot will land the airplane. And then, he will talk about the airplane.

94.
A) The mechanic will examine the car engine. But first, he will ask about the car engine.
B) The mechanic will examine the car engine. And then, he will ask about the car engine.
C) The mechanic will disassemble the car engine. But first, he will ask about the car engine.
D) The mechanic will disassemble the car engine. And then, he will ask about the car engine.

95.
A) The tailor will measure the pants. But first, he will ask about the pants.
B) The tailor will measure the pants. And then, he will ask about the pants.
C) The tailor will shorten the pants. But first, he will ask about the pants.
D) The tailor will shorten the pants. And then, he will ask about the pants.

96.
A) The new employee will stare at the cash register. But first, he will ask about the cash register.
B) The new employee will stare at the cash register. And then, he will ask about the cash register.
C) The new employee will open up the cash register. But first, he will ask about the cash register.
D) The new employee will open up the cash register. And then, he will ask about the cash register.

97.
A) The bicyclist will discover the flat tire. But first, she will complain about the tire.
B) The bicyclist will discover the flat tire. And then, she will complain about the tire.
C) The bicyclist will repair the flat tire. But first, she will complain about the tire.
D) The bicyclist will repair the flat tire. And then, she will complain about the tire.

98.
A) The angry music conductor will squeeze the baton. But first, he will complain about the baton.
B) The angry music conductor will squeeze the baton. And then, he will complain about the baton.
C) The angry music conductor will snap the baton. But first, he will complain about the baton.
D) The angry music conductor will snap the baton. And then, he will complain about the baton.

99.
A) The man will criticize the brochure. But first, he will read the brochure.
B) The man will criticize the brochure. And then, he will read the brochure.
C) The man will fold the brochure. But first, he will read the brochure.
D) The man will fold the brochure. And then, he will read the brochure.

100.
A) The illustrator will copy the cartoon. But first, he will display the cartoon.
B) The illustrator will copy the cartoon. And then, he will display the cartoon.
C) The illustrator will color the cartoon. But first, he will display the cartoon.
D) The illustrator will color the cartoon. And then, he will display the cartoon.

101.
A) The hunter will inspect the rifle. But first, he will frown at the rifle.

B) The hunter will inspect the rifle. And then, he will frown at the rifle.
C) The hunter will load the rifle. But first, he will frown at the rifle.
D) The hunter will load the rifle. And then, he will frown at the rifle.

102.
A) The woman will tap the table. But first, she will walk around the table.
B) The woman will tap the table. And then, she will walk around the table.
C) The woman will set the table. But first, she will walk around the table.
D) The woman will set the table. And then, she will walk around the table.

103.
A) The grocer will weigh the blueberries. But first, he will smell the blueberries.
B) The grocer will weigh the blueberries. And then, he will smell the blueberries.
C) The grocer will blend the blueberries. But first, he will smell the blueberries.
D) The grocer will blend the blueberries. And then, he will smell the blueberries.

104.
A) The man will touch the label. But first, he will read the label.
B) The man will touch the label. And then, he will read the label.
C) The man will remove the label. But first, he will read the label.
D) The man will remove the label. And then, he will read the label.

105.
A) The gym teacher will slap the basketball. But first, he will comment on the basketball.
B) The gym teacher will slap the basketball. And then, he will comment on the basketball.
C) The gym teacher will inflate the basketball. But first, he will comment on the basketball.
D) The gym teacher will inflate the basketball. And then, he will comment on the basketball.

106.
A) The contractor will measure the swimming pool. But first, he will walk around the pool.
B) The contractor will measure the swimming pool. And then, he will walk around the pool.
C) The contractor will drain the swimming pool. But first, he will walk around the pool.
D) The contractor will drain the swimming pool. And then, he will walk around the pool.

107.
A) The dog will lie beside the homework. But first, he will smell the homework.
B) The dog will lie beside the homework. And then, he will smell the homework.
C) The dog will tear up the homework. But first, he will smell the homework.
D) The dog will tear up the homework. And then, he will smell the homework.

108.

A) The boy will swing at the piñata. But first, he will laugh at the piñata.
B) The boy will swing at the piñata. And then, he will laugh at the piñata.
C) The boy will knock down the piñata. But first, he will laugh at the piñata.
D) The boy will knock down the piñata. And then, he will laugh at the piñata.

109.
A) The boy will show off the sand castle. But first, he will guard the sand castle.
B) The boy will show off the sand castle. And then, he will guard the sand castle.
C) The boy will finish up the sand castle. But first, he will guard the sand castle.
D) The boy will finish up the sand castle. And then, he will guard the sand castle.

110.
A) The hyena will creep behind the wildebeest. But first, it will growl at the wildebeest.
B) The hyena will creep behind the wildebeest. And then, it will growl at the wildebeest.
C) The hyena will run down the wildebeest. But first, it will growl at the wildebeest.
D) The hyena will run down the wildebeest. And then, it will growl at the wildebeest.

111.
A) The botanist will examine the plant. But first, he will document the plant.
B) The botanist will examine the plant. And then, he will document the plant.
C) The botanist will dissect the plant. But first, he will document the plant.
D) The botanist will dissect the plant. And then, he will document the plant.

112.
A) The man will choose the bagel. But first, he will smell the bagel.
B) The man will choose the bagel. And then, he will smell the bagel.
C) The man will slice the bagel. But first, he will smell the bagel.
D) The man will slice the bagel. And then, he will smell the bagel.

113.
A) The girl will inspect the stick of gum. But first, she will complain about the gum.
B) The girl will inspect the stick of gum. And then, she will complain about the gum.
C) The girl will chew the stick of gum. But first, she will complain about the gum.
D) The girl will chew the stick of gum. And then, she will complain about the gum.

114.
A) The trainer will pat the horse. But first, he will feed the horse.
B) The trainer will pat the horse. And then, he will feed the horse.
C) The trainer will saddle the horse. But first, he will feed the horse.
D) The trainer will saddle the horse. And then, he will feed the horse.

115.
A) The woman will look into the baby carriage. But first, she will kneel beside the baby carriage.
B) The woman will look into the baby carriage. And then, she will kneel beside the baby carriage.

C) The woman will fold up the baby carriage. But first, she will kneel beside the baby carriage.
D) The woman will fold up the baby carriage. And then, she will kneel beside the baby carriage.

116.
A) The man will check the wristwatch. But first, he will brag about the wristwatch.
B) The man will check the wristwatch. And then, he will brag about the wristwatch.
C) The man will reset the wristwatch. But first, he will brag about the wristwatch.
D) The man will reset the wristwatch. And then, he will brag about the wristwatch.

117.
A) The man will look for the cell phone. But first, he will gripe about the cell phone.
B) The man will look for the cell phone. And then, he will gripe about the cell phone.
C) The man will put away the cell phone. But first, he will gripe about the cell phone.
D) The man will put away the cell phone. And then, he will gripe about the cell phone.

118.
A) The boy will wait beside the Halloween costume. But first, he will ask for the costume.
B) The boy will wait beside the Halloween costume. And then, he will ask for the costume.
C) The boy will try on the Halloween costume. But first, he will ask for the costume.
D) The boy will try on the Halloween costume. And then, he will ask for the costume.

119.
A) The grandfather will look at the Thanksgiving turkey. But first, he will walk around the turkey.
B) The grandfather will look at the Thanksgiving turkey. And then, he will walk around the turkey.
C) The grandfather will cut up the Thanksgiving turkey. But first, he will walk around the turkey.
D) The grandfather will cut up the Thanksgiving turkey. And then, he will walk around the turkey.

120.
A) The woman will count the potatoes. But first, she will talk about the potatoes.
B) The woman will count the potatoes. And then, she will talk about the potatoes.
C) The woman will mash the potatoes. But first, she will talk about the potatoes.
D) The woman will mash the potatoes. And then, she will talk about the potatoes.

APPENDIX B

Experiment 2 event comprehension items (object varied, action fixed.. Full stimulus set of 100 items. Each subject saw each item in only one of the two conditions. All items contain the same verb in both conditions. Items 1-60 are matched across conditions as closely as possible on the specific action connotation of the verb.

A = action minimally changes object
B = action substantially changes object

1.
A) The girl will stomp on the penny. And then, she will look down at the penny.
B) The girl will stomp on the egg. And then, she will look down at the egg.

2.
A) The girl will jump on the soft grass. And then, she will ask about the grass.
B) The girl will jump on the cardboard box. And then, she will ask about the box.

3.
A) The teenager will drop the beach ball. And then, she will run away from the beach ball.
B) The teenager will drop the mayonnaise jar. And then, she will run away from the mayonnaise jar.

4.
A) The marksman will shoot at the old worn-out target. And then, he will point at the target.
B) The marksman will shoot at the brand new target. And then, he will point at the target.

5.
A) The girl will lick the heart-shaped lollipop. And then, she will put down the lollipop.
B) The girl will lick the postage stamp. And then, she will put down the stamp.

6.
A) The maid will scrub the pristine bathtub. And then, she will admire the bathtub.
B) The maid will scrub the grimy bathtub. And then, she will admire the bathtub.

7.
A) The angry boxer will punch the training bag. And then, he will glare at the training bag.
B) The angry boxer will punch the fatigued opponent. And then, he will glare at the fatigued opponent.

8.
A) The girl will pinch the Beanie Baby. And then, she will inspect the Beanie Baby.
B) The girl will pinch the Silly Putty. And then, she will inspect the Silly Putty.

9.
A) The man will squeeze the tennis ball. And then, he will frown at the tennis ball.
B) The man will squeeze the lemon wedge. And then, he will frown at the lemon wedge.

10.
A) The woman will sit on the leather couch cushion. And then, she will ask about the couch cushion.
B) The woman will sit on the inflated whoopee cushion. And then, she will ask about the whoopee cushion.

11.
A) The boy will step on the heavily trodden snow. And then, he will enjoy the snow.
B) The boy will step on the newly fallen snow. And then, he will enjoy the snow.

12.
A) The girl will stick her finger through the doughnut. And then, she will grin at the doughnut.
B) The girl will stick her finger through the cupcake. And then, she will grin at the cupcake.

13.
A) The woman will soak the damp washcloth. And then, she will inspect the washcloth.
B) The woman will soak the dry sponge. And then, she will inspect the sponge.

14.
A) The woman will heat up the frying pan. And then, she will wait beside the frying pan.
B) The woman will heat up the chocolate fondue. And then, she will wait beside the fondue.

15.
A) The groomer will brush the horse's shiny coat. And then, she will comment on the horse's coat.
B) The groomer will brush the horse's tangled mane. And then, she will comment on the horse's mane.

16.
A) The man will shake the empty champagne bottle. And then, he will joke about the champagne bottle.
B) The man will shake the unopened champagne bottle. And then, he will joke about the champagne bottle.

17.
A) The girl will kick the wall. And then, she will yell at the wall.
B) The girl will kick the football. And then, she will yell at the football.

18.
A) The girl will push on the granite statue. And then, she will walk away from the granite statue.
B) The girl will push on the desk chair. And then, she will walk away from the desk chair.

19.
A) The teenager will tip over the empty pudding container. And then, she will reach for the container.
B) The teenager will tip over the bowl of oatmeal. And then, she will reach for the oatmeal.

20.
A) The dog will chomp on the durable rawhide. And then, it will spit out the rawhide.
B) The dog will chomp on the soft treat. And then, it will spit out the treat.

21.
A) The girl will drop the deflated birthday balloon. And then, she will laugh about the birthday balloon.
B) The girl will drop the giant water balloon. And then, she will laugh about the water balloon.

22.
A) The dog will tug on the leather leash. And then, it will look back at the leash.
B) The dog will tug on the retractable leash. And then, it will look back at the leash.

23.
A) The farmer will prod the cow carcass. And then, he will complain about the carcass.
B) The farmer will prod the sleeping rooster. And then, he will complain about the rooster.

24.
A) The student will lie on the firm mattress. And then, she will get off of the mattress.
B) The student will lie on the new waterbed. And then, she will get off of the waterbed.

25.
A) The trainer will splash the dolphin. And then, she will watch the dolphin.
B) The trainer will splash the cat. And then, she will watch the cat.

26.
A) The toddler will poke the action figure. And then, he will inspect the action figure.
B) The toddler will poke the bobble-head doll. And then, he will inspect the bobble-head doll.

27.
A) The child will knock over the hard plastic cup. And then, he will run away from the cup.

B) The child will knock over the delicate flower vase. And then, he will run away from the vase.

28.
A) The child will squeeze the stress ball. And then, he will talk about the ball.
B) The child will squeeze the dried-up leaf. And then, he will talk about the leaf.

29.
A) The child will drop the soccer ball. And then, he will stand over the ball.
B) The child will drop the fragile ornament. And then, he will stand over the ornament.

30.
A) The girl will plug the empty bathtub. And then, she will walk away from the bathtub.
B) The girl will plug the draining bathtub. And then, she will walk away from the bathtub.

31.
A) The waiter will wipe the clean wine glass. And then, he will put down the wine glass.
B) The waiter will wipe the dirty wine glass. And then, he will put down the wine glass.

32.
A) The kitten will claw the scratching post. And then, it will hiss at the post.
B) The kitten will claw the new curtains. And then, it will hiss at the curtains.

33.
A) The teenager will drive over the speed bump. And then, she will look back at the speed bump.
B) The teenager will drive over the new skateboard. And then, she will look back at the skateboard.

34.
A) The man will lean on the sturdy fence. And then, he will grumble about the fence.
B) The man will lean on the precarious ladder. And then, he will grumble about the ladder.

35.
A) The toddler will splash the rubber ducky. And then, she will pick up the rubber ducky.
B) The toddler will splash the paper towel. And then, she will pick up the paper towel.

36.
A) The karate instructor will kick the foam pad. And then, he will hold up the pad.
B) The karate instructor will kick the wooden board. And then, he will hold up the board.

37.
A) The boy will pound the wooden table. And then, he will walk away from the table.
B) The boy will pound the wet clay. And then, he will walk away from the clay.

38.
A) The servant will fan the queen. And then, he will wait by the queen.
B) The servant will fan the fire. And then, he will wait by the fire.

39.
A) The toddler will squeeze the Barbie doll. And then, she will laugh at the Barbie doll.
B) The toddler will squeeze the frosting tube. And then, she will laugh at the frosting tube.

40.
A) The dog will lick its large furry paw. And then, it will sniff its paw.
B) The dog will lick the ice cream sundae. And then, it will sniff the sundae.

41.
A) The student will tap the wooden desk. And then, she will sit behind the desk.
B) The student will tap her sleeping friend. And then, she will sit behind her friend.

42.
A) The boy will shake the empty ketchup bottle. And then, he will hold the ketchup bottle.
B) The boy will shake the carbonated soft drink. And then, he will hold the soft drink.

43.
A) The waves will crash on the rock. And then, they will recede away from the rock.
B) The waves will crash on the sandcastle. And then, they will recede away from the sandcastle.

44.
A) The boy will stomp on the hardwood floor. And then, he will look down at the floor.
B) The boy will stomp on the cheap sunglasses. And then, he will look down at the sunglasses.

45.
A) The boy will bite down on the hard plastic mouthguard. And then, he will complain about the mouthguard.
B) The boy will bite down on the dental impression putty. And then, he will complain about the putty.

46.
A) The chef will boil the silverware. And then, she will complain about the silverware.
B) The chef will boil the spaghetti. And then, she will complain about the spaghetti.

47.
A) The hornet will sting the scarecrow. And then, it will circle around the scarecrow.
B) The hornet will sting the person. And then, it will circle around the person.

48.
A) The man will bump into the sofa. And then, he will stand beside the sofa.
B) The man will bump into the chandelier. And then, he will stand beside the chandelier.

49.
A) The hiker will drop the metal canteen. And then, she will reach for the canteen.
B) The hiker will drop the delicate camera. And then, she will reach for the camera.

50.
A) The girl will blow on the dice. And then, she will smile about the dice.
B) The girl will blow on the dandelion. And then, she will smile about the dandelion.

51.
A) The girl will step on the pebble. And then, she will notice the pebble.
B) The girl will step on the spider. And then, she will notice the spider.

52.
A) The man will microwave the coffee. And then, he will smell the coffee.
B) The man will microwave the popcorn. And then, he will smell the popcorn.

53.
A) The girl will drop the binder. And then, she will frown at the binder.
B) The girl will drop the laptop. And then, she will frown at the laptop.

54.
A) The puppy will gnaw on the lamb bone. And then, it will carry the lamb bone.
B) The puppy will gnaw on the stuffed animal. And then, it will carry the stuffed animal.

55.
A) The boy will shake up the empty water bottle. And then, he will put down the bottle.
B) The boy will shake up the settled orange juice. And then, he will put down the juice.

56.
A) The squirrel will hang on to the branch. And then, it will scamper away from the branch.
B) The squirrel will hang on to the clothesline. And then, it will scamper away from the clothesline.

57.
A) The bank robber will shoot at the armored vehicle. And then, he will run away from the vehicle.
B) The bank robber will shoot at the glass window. And then, he will run away from the window.

58.

A) The man will step on the cloth doormat. And then, he will look down at the doormat.
B) The man will step on the beer can. And then, he will look down at the can.

59.
A) The girl will poke the teddy bear. And then, she will laugh about the teddy bear.
B) The girl will poke the card tower. And then, she will laugh about the card tower.

60.
A) The maid will sweep the spotless floor. And then, she will stand on the floor.
B) The maid will sweep the dusty floor. And then, she will stand on the floor.

61.
A) The man will let go of the empty shopping cart. And then, he will look at the cart.
B) The man will let go of the compressed metal spring. And then, he will look at the spring.

62.
A) The boy will suck on the soup spoon. And then, he will spit out the soup spoon.
B) The boy will suck on the ice cube. And then, he will spit out the ice cube.

63.
A) The woman will heat up the plates. And then, she will chat about the plates.
B) The woman will heat up the water. And then, she will chat about the water.

64.
A) The horse will flick its tail. And then, it will look toward its tail.
B) The horse will flick the mosquito. And then, it will look toward the mosquito.

65.
A) The woman will beat the rug. And then, she will look closely at the rug.
B) The woman will beat the egg. And then, she will look closely at the egg.

66.
A) The girl will pluck the guitar. And then, she will hold on to the guitar.
B) The girl will pluck the flower. And then, she will hold on to the flower.

67.
A) The boy will push the closed bathroom door. And then, he will frown at the door.
B) The boy will push the lined up dominoes. And then, he will frown at the dominoes.

68.
A) The girl will poke the bunny rabbit doll. And then, she will laugh about the doll.
B) The girl will poke the chewing gum bubble. And then, she will laugh about the bubble.

69.

A) The man will chew the old mechanical pencil. And then, he will complain about the pencil.
B) The man will chew the piece of chicken. And then, he will complain about the chicken.

70.
A) The boy will bite his nails. And then, he will examine his nails.
B) The boy will bite the plum. And then, he will examine the plum.

71.
A) The chef will warm up the broccoli. And then, he will wait beside the broccoli.
B) The chef will warm up the butter. And then, he will wait beside the butter.

72.
A) The teenager will drive through the giant tunnel. And then, she will look back at the tunnel.
B) The teenager will drive through the giant puddle. And then, she will look back at the puddle.

73.
A) The boy will pull on the stuck window. And then, he will complain about the stuck window.
B) The boy will pull on the elastic band. And then, he will complain about the elastic band.

74.
A) The boy will crash the bumper car. And then, he will complain about the bumper car.
B) The boy will crash the remote-controlled car. And then, he will complain about the remote-controlled car.

75.
A) The woman will press the broken piano key. And then, she will ask about the piano key.
B) The woman will press the wrinkled dress shirt. And then, she will ask about the dress shirt.

76.
A) The woman will crush the pillow. And then, she will pick up the pillow.
B) The woman will crush the ice. And then, she will pick up the ice.

77.
A) The girl will bend her knees. And then, she will complain about her knees.
B) The girl will bend the paperclip. And then, she will complain about the paperclip.

78.
A) The boy will jiggle the bathroom door handle. And then, he will frown at the handle.

B) The boy will jiggle the stacked soda cans. And then, he will frown at the cans.

79.
A) The boy will step on to the tennis court. And then, he will walk off the court.
B) The boy will step on to the wet cement. And then, he will walk off the cement.

80.
A) The man will smoke the pipe. And then, he will comment on the pipe.
B) The man will smoke the cigar. And then, he will comment on the cigar.

81.
A) The girl will spin the colorful globe. And then, she will display the colorful globe.
B) The girl will spin the cotton candy. And then, she will display the cotton candy.

82.
A) The girl will squeeze her boyfriend's arm. And then, she will hold on to her boyfriend's arm.
B) The girl will squeeze the tube of toothpaste. And then, she will hold on to the tube of toothpaste.

83.
A) The man will flip the silver coin. And then, he will look closely at the coin.
B) The man will flip the half-done pancake. And then, he will look closely at the pancake.

84.
A) The girl will roll her eyes. And then, she will ask about her eyes.
B) The girl will roll the burrito. And then, she will ask about the burrito.

85.
A) The man will grill the suspect. And then, he will frown at the suspect.
B) The man will grill the pork. And then, he will frown at the pork.

86.
A) The boy will scratch his head. And then, he will complain about his head.
B) The boy will scratch the CD) And then, he will complain about the CD.

87.
A) The man will wind up the broken toy car. And then, he will complain about the toy car.
B) The man will wind up the knotted fishing line. And then, he will complain about the fishing line.

88.
A) The boy will scrape the pavement. And then, he will frown at the pavement.
B) The boy will scrape his knee. And then, he will frown at his knee.

89.
A) The boy will yank the rope swing. And then, he will comment on the swing.
B) The boy will yank the loose tooth. And then, he will comment on the tooth.

90.
A) The man will type on the new computer. And then, he will complain about the computer.
B) The man will type on the tax form. And then, he will complain about the form.

91.
A) The gymnast will curl the large heavy weight. And then, she will stare at the weight.
B) The gymnast will curl her long straight hair. And then, she will stare at her hair.

92.
A) The woman will roll her tongue. And then, she will admire her tongue.
B) The woman will roll the sushi. And then, she will admire the sushi.

93.
A) The woman will scratch the mosquito bite. And then, she will frown at the mosquito bite.
B) The woman will scratch the lottery ticket. And then, she will frown at the lottery ticket.

94.
A) The boy will pick his nose. And then, he will complain about his nose.
B) The boy will pick the scab. And then, he will complain about the scab.

95.
A) The man will snap the leather whip. And then, he will examine the whip.
B) The man will snap the plastic ruler. And then, he will examine the ruler.

96.
A) The boy will slap the basketball. And then, he will look at the basketball.
B) The boy will slap the grasshopper. And then, he will look at the grasshopper.

97.
A) The woman will check the parking meter. And then, she will ask about the parking meter.
B) The woman will check the answer box. And then, she will ask about the answer box.

98.
A) The man will chew on the plastic toothpick. And then, he will comment on the plastic toothpick.
B) The man will chew on the carrot stick. And then, he will comment on the carrot stick.

99.

A) The woman will deliver the mail. And then, she will talk about the mail.
B) The woman will deliver the baby. And then, she will talk about the baby.

100.
A) The woman will grind her teeth. And then, she will talk about her teeth.
B) The woman will grind the pepper. And then, she will talk about the pepper.

APPENDIX C

Experiment 3 state-change comprehension items Each subject saw each item in only one of the two conditions.

A = action minimally changes object
B = action substantially changes object

1.	A) sniff the flower	B) pluck the flower
2.	A) yell at the jack-in-the-box	B) pop open the jack-in-the-box
3.	A) reach for the apple	B) bite into the apple
4.	A) smile at the candy bar	B) unwrap the candy bar
5.	A) feel the egg	B) crack open the egg
6.	A) grip the hose	B) unravel the hose
7.	A) ask about the banana	B) peel the banana
8.	A) reach for the shoe	B) tie the shoe
9.	A) tap on the blackboard	B) draw on the blackboard
10.	A) comment on the umbrella	B) open the umbrella
11.	A) measure the jump rope	B) cut up the jump rope
12.	A) skim through the essay	B) mark up the essay
13.	A) laugh at the cartoon	B) color in the cartoon
14.	A) count the potatoes	B) mash the potatoes
15.	A) ask about the book	B) open up the book
16.	A) gripe about the bed	B) make up the bed
17.	A) weigh the pumpkin	B) carve the pumpkin
18.	A) sit in front of the candle	B) blow out the candle
19.	A) pick up the balloon	B) inflate the balloon

20.	A) marvel at the puzzle	B) break apart the puzzle
21.	A) stand beside the mannequin	B) dress up the mannequin
22.	A) step over the sleeping bag	B) roll up the sleeping bag
23.	A) touch the jewelry box	B) open the jewelry box
24.	A) sniff the onion	B) chop the onion
25.	A) sit next to the lamp	B) turn off the lamp
26.	A) step over the rug	B) unroll the rug
27.	A) blow on the pizza	B) slice the pizza
28.	A) touch the gingerbread man	B) decorate the gingerbread man
29.	A) tap the wine glass	B) crack the wine glass
30.	A) point at the tree	B) chop down the tree
31.	A) peer into the tent	B) take apart the tent
32.	A) bang on the cash register	B) open up the cash register
33.	A) touch the canvas	B) paint on the canvas
34.	A) tap on the table	B) set the table
35.	A) kneel beside the window	B) open up the window
36.	A) walk around the pool	B) drain the pool
37.	A) point at the piñata	B) knock down the piñata
38.	A) smell the bagel	B) slice the bagel
39.	A) kneel beside the baby carriage	B) fold up the baby carriage
40.	A) poke at the turkey	B) cut up the turkey